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Fish biology

DURATION OF FOOD EVACUATION IN HERRING, *CLUPEA HARENGUS* L., AND SPRAT, *SPRATTUS SPRATTUS* (L.)

CZAS EWAKUACJI POKARMU U ŚLEDZIA *CLUPEA HARENGUS* L. I SZPROTA *SPRATTUS SPRATTUS* (L.)

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The fish, which had fed under natural conditions, were kept in tanks and changes in stomach filling with time were observed. Linear relationships between filling and time at various temperatures and different initial filling are described. The relationships serve as a basis for multiple regression equations describing the relationship between food evacuation time and the two factors mentioned above. In the case of herring, separate equations were calculated for mesoplanktonic and makroplanktonic -benthic food.

INTRODUCTION

To determine food rations of fish under natural conditions it is necessary to know the metabolic intensity during feeding. Depending on a ration estimation method applied, metabolic intensity is expressed either as a rate of food evacuation from the digestive tract or by means of oxygen requirement indices. Both methods are in general use nowadays. The first was worked out by Bajkov (1935) and the other is based on energy budget equation given by Winberg (1956). To estimate the amount of food consumed by herring, Aneer (1980) and Lipskaja et al. (1980) used the second method. The results presented below served to achieve the same goal by means of the first method (Załachowski et al., 1976; Szypuła, 1982).

The difficulty in estimating the rate of food elimination from the fish digestive tract stems from the fact that the process is subject to multiple interactions and, actually, can be studied in detail in the laboratory only. In the case of marine fish, it has been possible to determine the multiple interactions the process is exposed to mainly in those species that can be kept without harm in aquaria for a long time, such as, e.g., the Gadidae (Jones, 1974) and flatfish (Jobling and Davies, 1970; Flowerdew and Grove, 1979). Delicate and vulnerable pelagic species, including sprat and herring, are difficult to keep for a long time and in dense concentrations in artificial habitats, thereby making data on digestion and food absorption difficult to obtain. The present work employs a combined, laboratory-field, method as suggested by Bajkov (1935). The gist of the method is natural feeding of the fish; they are subsequently caught and kept in tanks during which time they digest their food. The advantage of such an approach lies in the natural feeding conditions and natural food used, while among possible disadvantages one may count a stress caused by the rapid change of conditions during the experiment. Moreover, if the results are to be reliable, a large quantity of fish has to be examined, the number of samples and sample size increasing in proportion to the number of factors considered as influencing the evacuation process. The materials used in the present work allowed to consider effects of two variables: water temperature and initial filling of the stomach, the evacuation time being presented in function of these two variables. The kind of food was included in the case of herring. On the other hand, the fish were not differentiated in terms of their size; they were assumed to have attained commercial size, i.e., sexual maturity.

MATERIALS AND METHODS

The materials examined consisted of 1170 individuals of herring and 280 individuals of sprat, all caught in the Southern Baltic in 1973 and 1974. The fish were kept in onboard seawater tanks. Samples consisting of 10–15 individuals were collected at defined time intervals (1 h in summer, 3–5 h in the remaining seasons); the fishes were dissected, the food composition and weight determined, and a sample mean filling index ($M = \frac{w}{W} 10000$, where w = food weight; W = fish weight) calculated. For herring, separate indices were calculated for mesozooplankton (mainly the *Copepoda*) and for macroplankton and benthos (*Amphipoda, Isopoda, Mysidacea, Cumacea, Polychaeta, Chaetognatha, Pisces*) in order to check for possible differences in rates of elimination of these two groups of food items.

Food evacuation rate and duration were calculated, based on the assumption of linearity of the filling index-time relationship:

$$M = a + bt \quad (1)$$

where: M = filling index ($^0/_{000}$)
t = time (h)
a = initial filling of digestive tract ($^0/_{000}$)
b = evacuation rate coefficient (decrease in filling index after 1 h).

The values of a and b were calculated by the least squares method.

The duration of food evacuation (te) was determined by calculating t for M = 0 (that is the time after which the stomach filling will drop to zero: $te = -\frac{a}{b}$).

The relationship between the evacuation time, water temperature, and initial stomach filling is presented in the form of multiple regression equation:

$$tE = a_0 + a_1 T + a_2 Mo \quad (2)$$

where: tE = food evacuation time (h)
T = temperature (°C)
Mo = initial stomach filling ($^0/_{000}$).

The terms a_0, a_1, and a_2 were calculated by the least squares method. Theoretical time of food evacuation (tE) calculated with equation (2) was compared with the time te calculated with equation (1).

RESULTS

Tables 1–3 present changes in food evacuation rates and duration in herring and sprat. The analysis of data contained in the tables allows to conclude that the duration of food evacuation depends on temperature and on the initial filling of the digestive tract; additionally, the kind of food is important in herring.

Fig. 1 presents the mesoplankton evacuation rate in herring at various temperatures. As seen from slope coefficients of the regression equations, the mesozooplankton evacuation rate at 14.9°C is almost ten times that at 6°C.

Fig. 2 illustrates the mesozooplankton evacuation rate in herring as influenced by the initial filling, the temperature being held constant. Slope coefficients of the regression equations show that at a 21.18$^0/_{000}$ initial filling the rate of mesozooplankton elimination is higher than that at 4.68$^0/_{000}$ by a factor exceeding 3.

The evacuation rate of macroplankton and benthos consumed by herring is also closely dependent on temperature. As seen from Fig. 3, the rate of elimination of those items at 16.1°C is almost seven-fold higher than that at 6.6°C. The initial filling of the digestive tract affects the evacuation rate of macroplankton and benthos, too, similarly to the case of mesozooplankton. At an initial filling of 16.9$^0/_{000}$, macroplanktonic and benthic food items are eliminated from the stomachs at a rate exceeding that at 5.88$^0/_{000}$ by a factor of more than 4 (fig. 4).

Table 1

Mesozooplankton evacuation rate in herring, expressed as a reverse linear relationship (M = a + bt) between time (t) and stomach filling (M)

Temperature (°C)	No. of individuals examined	a	b	te	tE
2.5	125	3.49	−0.07	49.86	35.25
2.8	73	4.76	−0.18	20.70	34.53
2.9	78	4.68	−0.17	21.27	34.31
2.9	106	21.18	−0.54	39.22	34.49
3.1	82	7.76	−0.16	48.50	33.87
3.1	84	2.12	−0.06	35.33	33.81
6.0	80	1.87	−0.09	20.78	26.94
6.6	95	1.48	−0.07	21.14	25.52
12.0	60	110.40	−10.45	10.56	13.93
14.9	69	4.72	−0.91	5.19	5.90
15.8	101	2.04	−0.55	3.71	3.74
16.0	36	13.10	−4.60	2.85	3.38
16.0	56	52.16	−2.79	8.70	3.81
16.1	60	3.96	−1.04	3.81	3.05
16.2	65	0.65	−0.18	3.61	2.77

Fig. 5 shows temperature- and initial filling-dependent variability in mesozooplankton evacuation by sprat. At 16°C and 143.12$^0/_{000}$ initial filling, the mesoplankton is eliminated at a rate more than seven times that at 10.5°C and 30.46$^0/_{000}$.

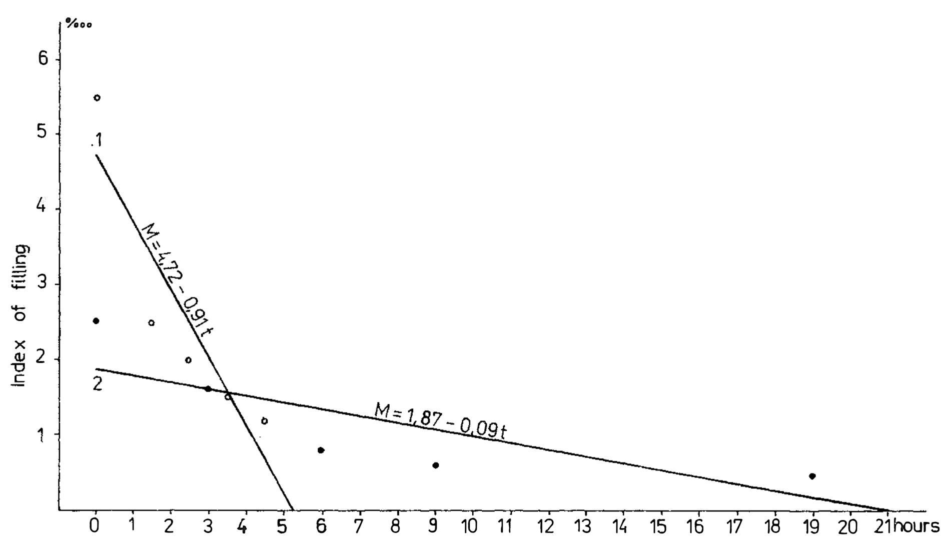

Fig. 1. Mesozooplankton evacuation rates in herring at various temperatures (1 = 14.9° C; 2 = 6.0°C)

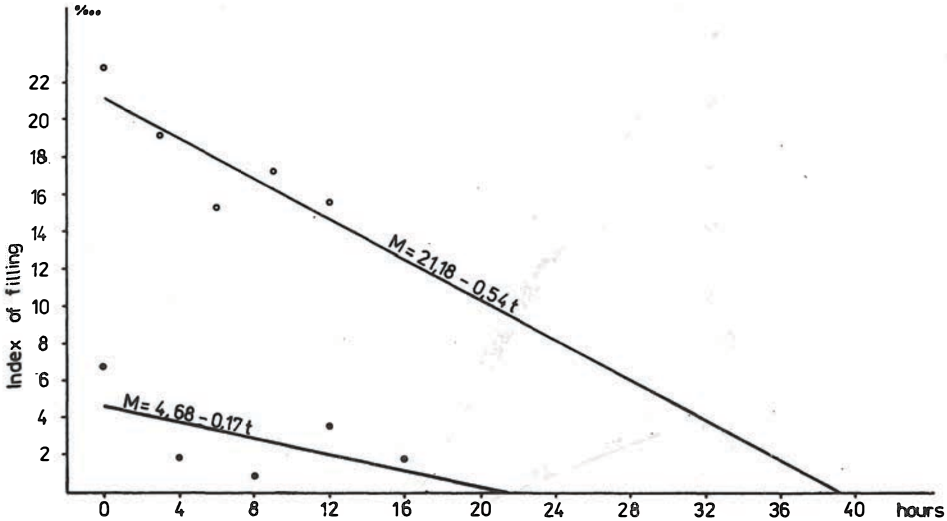

Fig. 2. Mesozooplankton evacuation rate in herring in function of initial stomach filling at constant temperature (2.9°C)

The examples given in Figs. 1–5 as well as the data in Tables 1–3 indicate a simple relationship to exist between the evacuation rate, temperature, and initial stomach filling: the higher the temperature and the larger the initial filling, the faster evacuation. On the other hand, the food evacuation time $(te = -\frac{a}{b})$ calculated from the initial filling (a) and evacuation rate coefficient (b) is in direct proportion to the initial filling and in inverse proportion to temperature. In order to illustrate the simultaneous relationship between the evacuation time, initial filling, and water temperature for both species in more detail, the following multiple regression equations were worked out:

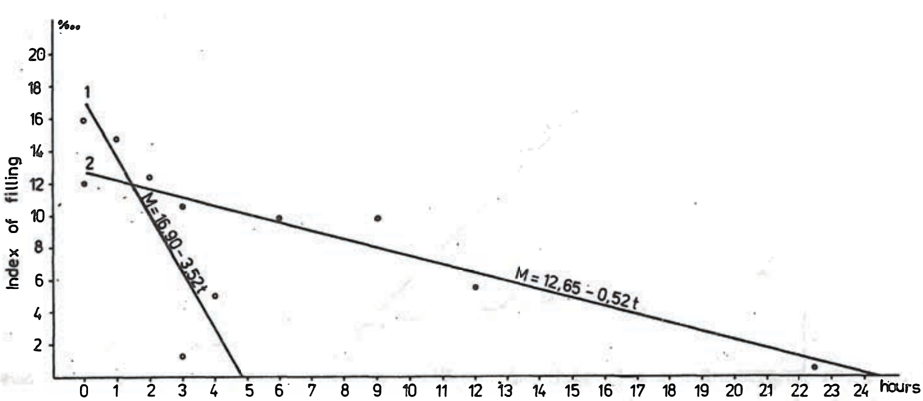

Fig. 3. Macroplankton and benthos evacuation rates in herring at various temperatures (1 = 16.1°C; 2 = 6.6°C)

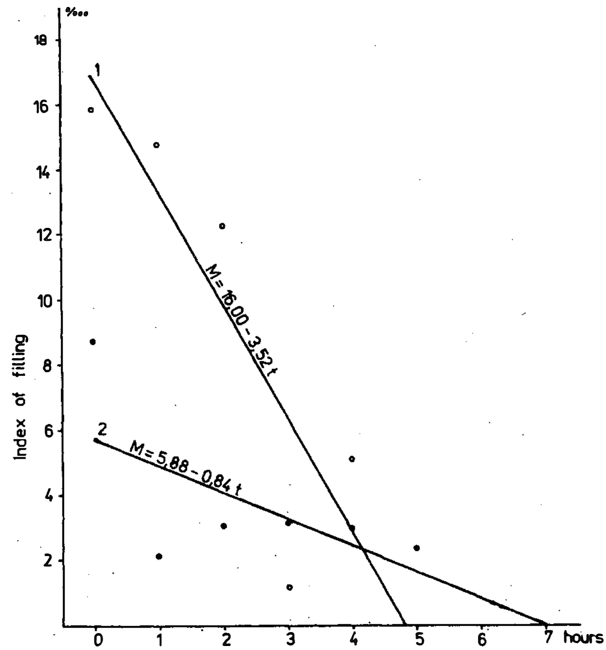

Fig. 4. Macroplankton and benthos evacuation rates in herring, in function of initial stomach filling at similar temperatures (1 = 16.1°C; 2 = 16.2°C)

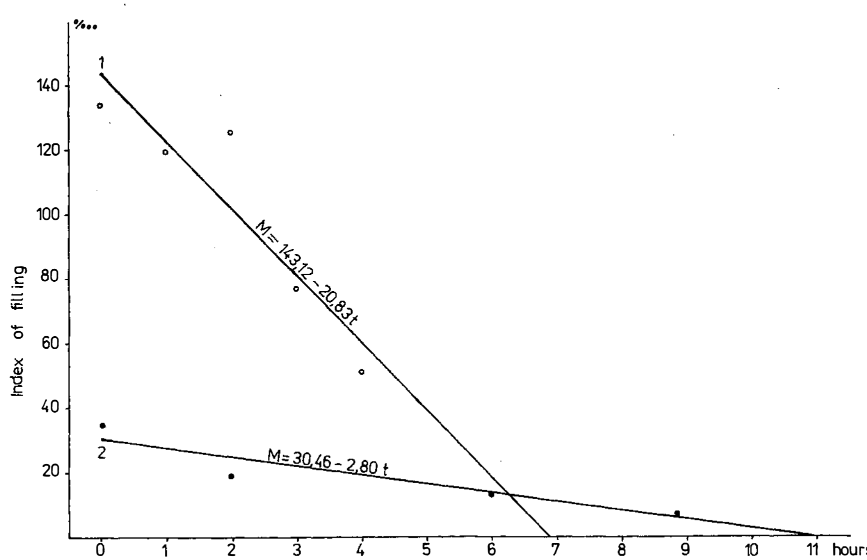

Fig. 5. Mesozooplankton evacuation rates in sprat at various temperatures (1 = 16.0°C; 2 = 10.5°C)

$$tE_1 = 41.128 - 2.368\ T + 0.011\ Mo$$
$$tE_2 = 35.141 - 2.034\ T + 0.321\ Mo$$
$$tE_3 = 62.380 - 5.587\ T + 0.238\ Mo$$

where tE_1, tE_2, and tE_3 denote mesozooplankton evacuation time in herring, macroplankton and benthos evacuation time in herring, and mesozooplankton evacuation time in sprat, respectively.

DISCUSSION

Properties of the function calculated are shown in Fig. 6 (lines 1–3). In the case of herring, noteworthy is the difference in evacuation time of mesozooplankton (2) and that of macroplankton and benthos (1). At a poor stomach filling, the times are almost identical; however, with increasing quantities of food to be digested, macroplankton and benthos tend to remain in the stomach longer and longer, the difference becoming more pronounced with increasing temperature. It is clear that the mesoplankton evacuation time depends mainly on temperature, the initial filling being of a minor importance

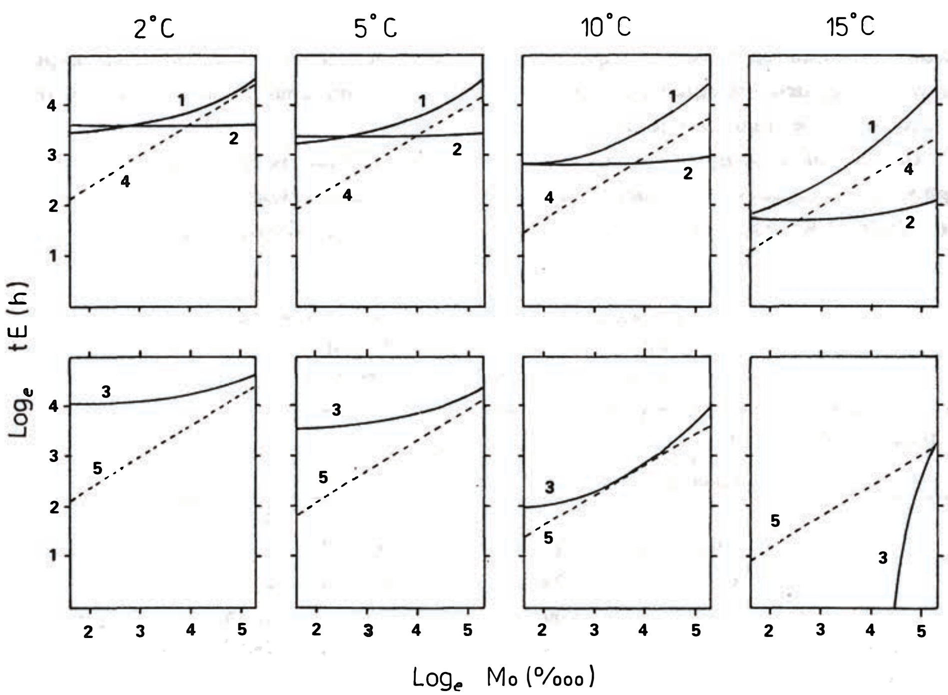

Fig. 6. Relationship between evacuation time (tE), initial filling (Mo), and temperature (T); 1 – 3: following the present multiple regression equations with tE_2, tE_1, tE_3, respectively; 4 and 5: following Tseitlin: $tE_4 = 69.8 \cdot 80^{0.26}\ (0.0001\ Mo)^{0.62} \exp[0.0806\ (20 - T)]$
$tE_5 = 84.1 \cdot 15^{0.34}\ (0.0001\ Mo)^{0.62} \exp[0.0806\ (20 - T)]$

($a_2 = 0.011$). That means, however, that an increase in filling has to result in a strong acceleration of evacuation. The effect, described also in other fish species (Windell, 1967) is explained by digestive enzymes secretion and peristaltic movements intensity being stimulated by an increasing pressure on stomach and intestine walls (Jobling and Davies, 1979). The curves compared (1 and 2) indicate the efficiency of the process in herring to be in inverse proportion to individual size of organisms eaten. When the digestive tract is densely packed with large macroplanktonic and benthic animals, an increase in temperature will accelerate the evacuation only slightly.

Reliability of the results that can be obtained by means of the multiple regression equations is difficult to ascertain due to a lack of comparable data on the two species under study. The results obtained give a good fit to the initial data, as evidenced by small differences between te and tE (Tables 1–3). Such a test may be, however, insufficient when the independent variables of the functions take up values from beyond the range of the experimental values, as exemplified by the function calculated for sprat. Although the function yielded the lowest te – tE differences (Table 3), it was calculated from 5 experiments only, four at about 11°C, and one at 16°C, but at a high initial filling index. As a result, at 15°C the function gives negative tE values at filling lower than $90^0/_{000}$, which means that its applicability is limited. This limitation is not a particularly significant one, as the sprat feed very intensely at higher temperatures; none the less, to render the equation more widel applicable, further experimental work is needed. Szypuła (1982), who used the equation in its form presented here, assumed the evacuation time not to be shorter than two hours.

An attempt to verify the equations presented can be made from results obtained when applying the equations to diel ration estimations (Załachowski et al., 1976; Szypuła, 1982). The results were obtained with Bajkov's method (Bajkov, 1935), and the

Table 2

Macroplankton and benthos evacuation rate in herring, expressed as a reverse linear relationship (M = a +bt) between time (t) and stomach filling (M)

Temperature (°C)	No. of individuals examined	a	b	te	tE
2.5	125	45.12	–0.95	47.49	44.54
2.9	78	0.84	–0.02	42.00	29.51
2.9	106	3.25	–0.14	23.21	30.29
3.1	82	8.00	–0.35	22.86	31.40
6.0	80	0.74	–0.03	24.67	23.17
6.6	95	12.65	–0.52	24.33	25.78
15.8	101	3.33	–0.76	4.38	4.07
16.1	60	16.90	–3.52	4.80	7.82
16.2	65	5.88	–0.84	7.00	4.08

Table 3

Mesozooplankton evacuation rate in sprat, expressed as a reverse linear relationship (M = a + bt) between time (t) and stomach filling (M)

Temperature (°C)	No. of individuals examined	a	b	te	tE
10.5	162	30.46	−2.84	10.73	10.97
10.8	15	15.05	−3.25	4.63	5.62
11.0	31	32.13	−3.58	8.97	8.57
11.5	56	37.45	−4.64	8.07	7.04
16.0	16	143.12	−20.83	6.87	7.05

comparable data for herring are those reported by Aneer (1980) and Lipskaja et al. (1980) as based on the equation given by Winberg (1956). Nagięć and Martyniak (1974) succeeded in their attempt to compare diel food rations of pikeperch as calculated by methods of Bajkov and Winberg. Working on herring, Aneer (1980) estimated diel rations to amount to 1.2–1.9% of the body weight, which agrees well with our results (Załachowski et al., 1976; Szypuła, 1982), while Lipskaja et al. (1980) arrived at much higher values: 5.8–7.6%. The latter are close to the data reported by De Silva and Balbontin (1974) for herring aged one year and feeding ad libitum; it is highly improbable though, that mature herring would feed with such an intensity under natural conditions.

Tseitlin (1980) proposed an equation relating the evacuation time to temperature, initial filling, and fish size. The equation concerns various meso- and/or bathypelagic species, its parameters being given in three versions corresponding to thermal sensitivity of cold- and warm-water species and intemediate ones. To compare the present results with those yielded by Tseitlin's equation, a mean fish weight had to be set at 80 g (herring) and 15 g (sprat). The functions obtained from Tseitlin's equation are plotted with dashed lines in Fig. 6. For herring, the graph (line 4) shows the course of a function calculated for intermediate species. The graph agrees with the results of the present multiple regressions at initial filling larger than 50⁰/₀₀₀ (even starting from 20⁰/₀₀₀ at higher temperatures), the Tseitlin's equation-based function, however, taking up the values intermediate to those obtained for mesozooplankton and macroplankton-benthos. At lower filling values, the present study points out to a dependence of evacuation time on portion size much weaker than would result from Tseiltin's formula. A similar comparison carried out for sprat shows Tseitlin's equation to yield values closest to the present ones in its warm-water species version (line 5 in Fig. 6). The similarity of the results appears to be lower than in the case of herring. If, however, only such a range of values of independent variables is considered as that used in the experiment (10°C or large initial filling at 15°C), the two functions compared turn out to yield similar times of food evacuation.

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CZAS EWAKUACJI POKARMU U ŚLEDZIA *CLUPEA HARENGUS* L. I SZPROTA *SPRATTUS SPRATTUS* (L.)

STRESZCZENIE

W latach 1973 i 1974 wykonano na statku badawczym 20 doświadczeń polegających na przetrzymywaniu śledzi i szprotów – bezpośrednio po złowieniu – w basenach z filtrowaną wodą morską. W doświadczeniach użyto łącznie 1450 ryb. W każdym doświadczeniu oznaczano średnie początkowe napełnienie przewodów pokarmowych (w $^0/_{000}$ w stosunku do ciężaru ryb), a następnie średnie napełnienie w określonych odstępach czasu, dostosowanych do pory roku. W przypadku

śledzia określano oddzielnie napełnienie mezoplanktonem oraz makroplanktonem i bentosem. Przyjmując, że zależność stanu napełnienia od czasu jest zbliżona do prostoliniowej (rys. 1–5), wyliczono równania:

$$M = a + bt$$

(gdzie: M = wskaźnik napełnienia ($^0/_{000}$), t = czas (godziny), a = początkowe napełnienie ($^0/_{000}$), b = współczynnik tempa ewakuacji), a także czas ewakuacji $te = -\frac{a}{b}$, dla wszystkich doświadczeń (tab. 1–3). Okazało się, że tempo i czas ewakuacji zależą zarówno od temperatury (rys. 1,3,5) jak i początkowego napełnienia (rys. 2 i 4). Zależność tę wyrażono za pomocą równań regresji trzy-cechowej otrzymując:

dla śledzia żywiącego się mezoplanktonem:

$$tE_1 = 41{,}128 - 2{,}368T + 0{,}011\,Mo$$

dla śledzia żywiącego się makroplanktonem i bentosem:

$$tE_2 = 35{,}141 - 2{,}034\,T + 0{,}321\,Mo$$

dla szprota żywiącego się mezoplanktonem:

$$tE_3 = 62{,}380 - 5{,}587\,T + 0{,}238\,Mo$$

gdzie: tE = czas ewakuacji (godziny), T = temperatura (^{o}C), Mo = napełnienie początkowe ($^0/_{000}$).

Różnica pomiędzy czasem ewakuacji mezoplanktonu i makroplanktonu z bentosem u śledzia wzrasta proporcjonalnie do wzrostu napełnienia początkowego i temperatury w sposób przedstawiony na rysunku 6 (linie 1 i 2). Wynika ona z tego, że przy silnym napełnieniu żołądka drobnymi formami mezoplanktonu tempo ewakuacji jest znacznie szybsze niż w przypadku równie silnego wypełnienia większymi organizmami makroplanktonu i bentosu.

Oba równania dla śledzia mają zastosowanie uniwersalne, natomiast równie dla szprota można stosować w warunkach zbliżonych do tych jakie zostały uwzględnione w doświadczeniach (tab. 3), to znaczy przy temperaturze 10–11^{o}C, a w wyższej tylko przy dużych napełnieniach.

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ВРЕМЯ ЭВАКУАЦИИ КОРМА У СЕЛЬДИ CLUPEA HARENGUS L. И ШПРОТА SPRATTUS SPRATTUS (L.)

Р е з ю м е

В 1973 и 1974 гг. на опытном судне были поставлены 20 опытов, касавшихся выдерживания сельди и шпрота - непосредственно после улова - по басеейнам заполненных морской пофильтрационной водой. Материалом для опыта служили 1450 штук рыбы. В рамках каждого опыта определяли в среднем: начальное заполнение желудочно-кишечного тракта (0/000 по отношению к весу рыбы), а затем заполнение за определенные промежутки времени, приспособленные к временам года. Для сельди в отдельности определяли заполнение мезопланктоном, а также макропланктоном и бентосом. Принимая во внимание, что зависимость состояния заполнения от времени приблизительно прямолинейная (рис.1-5), вычисляли уравнения:

$$M + a + bt$$

(где: M - показатель заполнения (0/000), t - время (часа), a - начальное заполнение (0/000), b - коэффициент темпа эвакуации), а также время эвакуации $te = -\frac{a}{b}$, для всех опытов (таб.1-3). Установлено, что темп и время эвакуации зависели, как от температуры (рис.1,3,5), так и от начального заполнения (рис.2 и 4). Эту зависимость представляет собой регрессионное уравнение с тремя признаками, а именно: для сельди кормившейся мезопланктоном:

$$TE_1 = 41{,}128 - 2{,}368T + 0{,}011Mo$$

для сельди кормившейся макропланктоном и бентосом:

$$tE_2 = 35{,}141 - 2{,}034T + 0{,}321Mo$$

для шпрота кормившегося мезопланктоном:

$$tE_3 = 62{,}380 - 5{,}587T + 0{,}238Mo$$

где: tE - время эвакуации (часа), T - температура (^{o}C), Mo - начальное заполнение (0/000).

Различия между временами эвакуации мезопланктона и макропланктона с бентосом у сельди увеличивались пропорционально, по мере повышения степени начального заполнения и температуры, что изображает рис.6 (линии 1 и 2). Полученные результаты показали, что при интенсивном заполнении желудка мелкими формами мезопланктона темп эвакуации является значительно большим по сравнению с таким же заполнением желудка более крупными организмами макропланктона и бентоса.

Оба уравнения для сельди имеют универсальное применение, тогда как уравнение для шпрота может применяться в условиях сходных с установленными для опыта (таб.3), т.е. при температуре 10-11^{o}C и при повышенной температуре для большого заполнения.

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