FISHERIES RESEARCH BOARD OF CANADA
Translation Series No. 1846

Distribution and food of ichthyoneuston in the subtropical NE Atlantic

by Jurgen Hartmann

Original title: Verteilung and Nahrung des Ichthyoneuston im subtropischen Nordostatlantik

From: "Meteor" Forschungwergenbnisse ("Meteor" Research Results) 8: 1-60, 1970

Translated by the Translation Bureau(ES)
Foreign Languages Division
Department of the Secretary of State of Canada

Fisheries Research Board of Canada
Marine Ecology Laboratory
Dartmouth, N. S.

1971

147 pages typescript

DEPARTMENT OF THE SECRETARY OF STATE
TRANSLATION BUREAU

FOREIGN LANGUAGES DIVISION

CANADA

SECRÉTARIAT D'ÉTAT
BUREAU DES TRADUCTIONS

DIVISION DES LANGUES ÉTRANGÈRES

TRANSLATED FROM – TRADUCTION DE	INTO – EN
German	English

AUTHOR – AUTEUR

Jürgen Hartmann

TITLE IN ENGLISH – TITRE ANGLAIS

Distribution and food of ichthyoneuston in the subtropical NE Atlantic

Title in foreign ~~language~~ ~~(transliterate foreign characters)~~

Verteilung und Nahrung des Ichthyoneuston im subtropischen Nordostatlantik

REFERENCE IN FOREIGN LANGUAGE (NAME OF BOOK OR PUBLICATION) IN FULL. TRANSLITERATE FOREIGN CHARACTERS.
RÉFÉRENCE EN LANGUE ÉTRANGÈRE (NOM DU LIVRE OU PUBLICATION), AU COMPLET. TRANSCRIRE EN CARACTÈRES PHONÉTIQUES.

"Meteor" Forschungsergebnisse

REFERENCE IN ENGLISH – RÉFÉRENCE EN ANGLAIS

"Meteor" Research Results

PUBLISHER – ÉDITEUR	DATE OF PUBLICATION / DATE DE PUBLICATION			PAGE NUMBERS IN ORIGINAL / NUMÉROS DES PAGES DANS L'ORIGINAL
not stated	YEAR / ANNÉE	VOLUME	ISSUE NO. / NUMÉRO	1-60
PLACE OF PUBLICATION / LIEU DE PUBLICATION				NUMBER OF TYPED PAGES / NOMBRE DE PAGES DACTYLOGRAPHIÉES
Berlin & Stuttgart, Germany	1970	Series D	8	147

REQUESTING DEPARTMENT / MINISTÈRE-CLIENT: Fisheries & Forestry

TRANSLATION BUREAU NO. / NOTRE DOSSIER Nº: 0222

BRANCH OR DIVISION / DIRECTION OU DIVISION: Fisheries Research Board ~~Marine Ecology Laboratory~~

TRANSLATOR (INITIALS) / TRADUCTEUR (INITIALES): E.S.

PERSON REQUESTING / DEMANDÉ PAR: Dr. J.J. Conover, Dartmouth, N.S.

DATE COMPLETED / ACHEVÉ LE: AUG 30 1971

YOUR NUMBER / VOTRE DOSSIER Nº: 769-18-14

DATE OF REQUEST / DATE DE LA DEMANDE: April 8, 1971

UNEDITED TRANSLATION
For information only
TRADUCTION NON REVISEE
Information seulement

DEPARTMENT OF THE SECRETARY OF STATE
TRANSLATION BUREAU
FOREIGN LANGUAGES DIVISION

SECRÉTARIAT D'ÉTAT
BUREAU DES TRADUCTIONS
DIVISION DES LANGUES ÉTRANGÈRES

CANADA

CLIENT'S NO. Nº DU CLIENT	DEPARTMENT MINISTÈRE	DIVISION/BRANCH DIVISION/DIRECTION	CITY VILLE
769-18-14	Fisheries & Forestry	Fisheries Research Board Marine Ecology Laboratory	Dartmouth, N.
BUREAU NO. Nº DU BUREAU	**LANGUAGE LANGUE**	**TRANSLATOR (INITIALS) TRADUCTEUR (INITIALES)**	**DATE**
0222	German	E.S.	AUG 3 0 1971

Reference: Jürgen Hartmann; Verteilung und Nahrung des Ichthyoneuston im subtropischen Nordostatlantik. "Meteor" Forschungsergebnisse, Series D, No. 8, pp. 1-60; Berlin and Stuttgart, December 1970.

Distribution and food of ichthyoneuston in the subtropical NE Atlantic

By Jürgen Hartmann*

With 25 illustrations and 10 Tables throughout text

Abstract

In four microlayers of the uppermost 60 cm of the subtropical NE Atlantic 477 samples of ichthyoneuston were collected. In at least 3 samples 34 groups (different taxa) of fish were discovered in the 0—10 cm layer. Among these groups there were 8 species of Beloniformes and 9 species of Myctophidae. Most of the fish were juveniles of 6—80 mm total length. — The regional distribution, the vertical macrodistribution in 6 layers of the upper 200 m, 3 patterns of vertical microdistribution, 6 patterns of diurnal migration, and 4 patterns of feeding activity are described. — Most of the fish found in the 0—10 cm layer by day were small in size and appeared only in a few specimens per haul. — The catches in the 0—10 cm microlayer were richer than those of the 10—25 cm microlayer, but poorer than those of the 0—30 m macrolayer. — According to their gut contents the fish living at the surface could be divided into 3 main groups. In respect of the size and quality of food items, a competition for food was calculated. — There is some evidence for a scarcity of food at the surface of the open subtropical Atlantic especially by day.

*) The manuscript has been completed in October 1969 at the Institute for Oceanography in Kiel (Germany). Present address of author: I — 80077 Ishia Porto. Villa Acquario — Italy.

Table of contents

cont'd on
next page

Table of Contents (cont'd.)

Foreword

Food shortage throughout the horse-latitude region of the open Atlantic Ocean poses for the fry, who depend upon a relatively dense supply of suitably sized planton, the problem of finding adequate nourishment. If food supply falls short of a certain density, the animal is condemned to starvation. However, adequate density of food stores does not have to be distributed evenly throughout the entire water column populated by young stages. It suffices for their survival if suitable "pastures" with adequate plankton density exist, on which they can graze at regular intervals.

Under his first impression of relatively plankton-rich samples obtained from the surface layer (0-15 cm) of the subtropical NE Atlantic, Professor Hempel suspected the existence of such a pasture for subtropical fry in the pelagic cover layer, which is several centimeters thick. With the purpose of checking out this hypothesis — which did not hold true — surface plankton has been sampled in April and June/July of 1967 during two cruises of the "Meteor" in the sea region between the Portuguese-Moroccan coast and 30° West. For comparison, additional material was collected with the vertically fishing Helgoland larvae net.

In 1968, the "Meteor" undertook another research cruise into NW African waters. This cruise provided an opportunity for complementary neuston sampling especially in the upwelling area off Mauretania.

In addition to a description of nutritional conditions prevailing close to the sub-surface, a presentation was required also of the vertical and horizontal, as well as the daily and seasonal distribution of fish larvae and young stages that roam the pelagic surface of the area chosen for this investigation.

Professor HEMPEL assigned the evaluation of the abundant material to doctorand WEIKERT and myself; Mr. WEIKERT has been entrusted with investigating the invertebrates, while the present work, which represents the main part of a thesis (HARTMANN 1969a), describes the ichthyoneuston with special emphasis on food intake.

My thanks are due, first of all, to Professor Dr. HEMPEL for having assigned to me such an interesting problem, and for his assistance in many respects. I also wish to thank the "Deutsche Forschungsgemeinschaft" (German Research Association) who made it possible for me to participate in both 1967 plateau cruises as well as in the 1968 West-Africa voyage of the R.V. "Meteor", and granted a scholarship. Dr. KINZER kindly provided larvae-net samples obtained in 1967, as well as the larvae net with alternating bucket mechanism, for which I express sincere thanks. I also wish to thank Mr. MAUL (Madeira), Dr. NELLEN (Kiel), and Dr. AHLSTROM (La Jolla), for the determination of sample specimens, and for providing literature and references. My co-doctorand, Mr. WEIKERT, eased the burden of evaluating the literature by translating numerous Slavic publications. My thanks are due also to the crew of the "Meteor", and to the biologists who assisted in sampling the material. Mr. LÜBKE took great care in drawing the illustrations.

The present work is limited to the investigation of fish types inhabiting the neuston.

The biotope of the neuston should not be designated as "hyponeuston" (ZAITSEV 1968, p. 18), nor as "neustal", or "hyponeustal", since we are dealing here with one and the same "narrow borderzone of the pelagic domain" which is, according to FRIEDRICH (1965) to be designated as "pleustal". Whoever wishes to speak of the biotope of the submerged neuston as of "the neustal" should consider that, then, the genus Halobates (epineuston) would remain outside the range of this "neustal". Who, on the other hand, includes in the designation "neustal" the air which interfaces the sea surface, depicts thus the actual biotope of the pleuston as "neustal". — ZAITSEV (1968) postulated on the basis of direct observations that, generally, the following thickness exists for the layer occupied by neuston: 1-3 cm for agitated sea, and 1-5 mm while surface is calm. While these limits may apply to oceanic microneuston, they surely do not apply to macro- and megaloneuston which may nevertheless constitute a considerable part of the ichthyoneuston. In this work, the term "pleustal" depicts the particular layer that was fished by the uppermost net utilized (Fig. 1), namely the 0-15 cm surface level.

1.2 Formulation of the problem

An introduction to marine neustonology and first results have been furnished by ZAITSEV in 1968.

Besides ZAITSEV, who concentrated his investigations on the Black Sea (1959-1968), it was PARIN (1967) who also specialized in the investigation of marine ichthyoneuston, but he studied the ichthyoneuston of the Pacific Ocean. ZAITSEV was primarily concerned with substantiating that the uppermost centimeters of the Black Sea are inhabited by a fauna that is qualitatively and quantitatively distinct from the plankton of lower layers. He observed, within the uppermost microlayer of 5 cm thickness, surprizingly marked maxima for eggs, larvae, and juvenile fish, as well as for invertebrates (for methods employed by ZAITSEV, cf. Table 1 (p. 11).

ZAITSEV's and PARIN's specialized works did not include the ecological role of the pleuston as a fish pasture, although — on the basis of dense hauls from the surface of the Black Sea — ZAITSEV attached great importance to the pleuston as feeding ground for fishes.

The present work is designed particularly for the determination of the importance held by the pleuston as a grazing place for the fish. However, the analyses of intestinal contents, which stand in the foreground of these investigations, cannot be considered separately. Obviously, food intake must be viewed in connection with other behavioral facttors of ichthyoneuston. Thus, PARIN (1967) considered a relationship between diurnal migration and feeding rhythm of neuston fishes. Therefore, the vertical, horizontal, daily, and seasonal distribution of ichthyoneuston will here also be taken into consideration.

Furthermore, it shall be determined of which species and stages the ichthyoneuston is composed. Since, in addition, a relationship between food supply and the abundance of fish was suspected, this raised also the question of possible aggregations in the pleustal layer.

The analyses of intestinal contents will show, according to type, amount and size, how plankton is distributed among the species and stages of grazers, and at what times of day food is taken by the individual groups. From these factors, a clear picture should emerge of the competition for food among ichthyoneuston.

In the closing chapter, the question of the nutritional capacity of the pleuston in the subtropical Atlantic will again be dealt with by taking all individual results into consideration. p.4

The invertebrates among the sampled material are presently (1969) being studied by WEIKERT, whose preliminary results have, in part, been taken into consideration in the present publication.

2. Materials and methods

2.1 Sampling devices

The features of an ideal sampling device for neuston have been described before by DAVID (1965a), and SAMEOTO & JAROSZYNSKI (1969). Because of low manufacturing costs, manageability, fast towing speed (?) and other advantages, the type of net developed by SAMEOTO & JAROSZYNSKI (1969), which is secured to a surfboard (see Table 1, p. 11), recommends itself as the future standard apparatus.

The most important devices that had been utilized for neuston sampling by 1965, were summarized at that time by DAVID (1965a). Table 1 describes modern models that are suited for the collection of ichthyoneuston. The first efficiently performing neuston sampling devices were developed by SAVILOV (1955) and ZAITSEV (1957). Another newly constructed apparatus was utilized by DELLA CROCE (1961).

DAVID (1965) introduced a new prototype which underwent several modifications (by HEMPEL 1967; PENNELL 1967; among others). By HEMPEL further improved models of DAVID's neuston glider were used in 1967 and 1968 on the "Meteor".

Two types of sampling apparatus can be distinguished: There are the nets devised by SAVILOV, ZAITSEV, and MARINARO on the one hand, which are operated from a drifting or anchored ship. On the other hand, the constructions of DELLA CROCE, DAVID, PENNELL, BIERI, HEMPEL, BARTLETT, BEN YAMI et al., and SAMEOTO are designed to be towed by a vessel in motion.

The slow sampling speed (appr. 1 knot) of the models mentioned first permits utilization of a wide-mouthed net — a possibility which found its realization in the devices of SAVILOV (net opening 100 x 60 cm), and ZAITSEV (net opening up to 300 x 25 cm). Furthermore, drifting devices allow the use of a finer mesh for the net. Another advantage is offered by the fact that these devices leave the water surface relatively undisturbed unless the lee whirl close to the drifting ship is being included in the sampling activity, as preferred by SAVILOV.

Devices towed under engine power have the advantage of higher net speed, which comes to 2 knots with DELLA CROCE's apparatus, 6 knots for those of DAVID, HEMPEL, and BARTLETT, and even to 11 knots for that of SAMEOTO. Probably, it was due merely to slow-speed towing that PARIN, who used SAVILOV's PT-1 apparatus (1 knot) failed to detect any rhythm in the diurnal migration of <u>Scomberesox saurus</u> which was observed, however, in the Atlantic Ocean with the aid of HEMPEL's glider (6 knots) (cf. 4.32, p. 45): It can be assumed that the larger <u>Scomberesox saurus</u> managed to avoid PARIN's slow-moving apparatus.

An important novelty was introduced by DAVID in that the towing structure is guided with an asymmetrical bridle* to either side of the ship so that the net fishes in quiet water, not disturbed by the turbulence caused by the ship's propeller.

---

*) <u>Translator's note</u>: The term "bridle" is used by DAVID (1965) in his paper describing his "Neuston Net".

The devices of ZAITSEV accomplish an absolute minimum of immersion of 5 cm. Immersion of other oceanic sampling devices is deeper: 10 cm (DAVID, BIERI, PENNELL, HEMPEL, BARTLETT), and 20-30 cm SAVILOV, BEN YAMI et al.).

DELLA CROCE covered the microstratification by fishing several layers consecutively with the same net. The arrangement of several nets on a ladder-like frame, thus sampling simultaneously 5 (ZAITSEV), 3 (DAVID, PENNELL), and 2 (HEMPEL, MARINARO) layers, does of course work more precisely.

The sampling devices utilized in the 1967 and 1968 investigations described here were developed by HEMPEL, but were based on DAVID's model. Since the model used in 1967 was made of heavy mahogany, it was equipped with additional floats, made of styropore and affixed underneath the skis, thus differing from DAVID's neuston net.

Initially, only the top net was in operation. Later, a second net of equal size was firmly attached to a metal frame; it thus fished simultaneously beneath the top net at a depth of appr. 45 cm. Finally, this so-called "lower net" was supplemented with a middle net situated directly adjacent to the top net (Fig. 1).

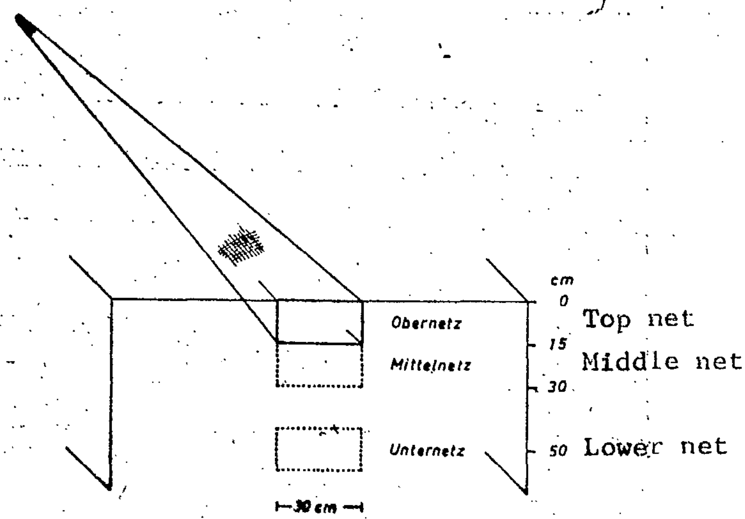


Fig. 1. Arrangement of the net openings (1967), upper **net mouth submerged.**

Table 1. Modern devices for the sampling of ichthyoneuston. — p. 5

Where author's name or sampled region is enclosed in parentheses, this refers to material which had also been collected with that particular type of equipment. SPECCHI (1968) and FENAUX (1968) came to the author's attention only after this Table was already in press.

Author	Designation	Submergence of top net (cm)	Net mouth width (cm)	Net speed (knots)	Layers fished (Quantity)	No. of nets fishing simultaneously (Quantity)	Position in relation to ship	Region sampled
SAVILOV (PARIN)	PT 1	25	100	drifting or anchored	1		close to ship in lee whirl	Pacific, Indian Ocean
ZAITSEV (DANIELSEN)	NT 3	5	300				abaft	Black Sea (N-Atlantic)(Medit.)
(GHIRARDELLI)	PNC-5		60		5			
DELLA CROCE	—	10	—	2	10	1	towed after	Mediterranean Sea
DAVID	Neuston net		30	5–6	1		sideways downside ship	Antarctica Indian Ocean Atlantic Ocean
			76					
			[illegible]	—	3			
PENNELL	—		20	5–6				
HEMPEL			30		4	2		North Atlantic
BIERI	Booby II		32	3	1			Pazific
MARINARO			40		2		hauled in by hawser	Mediterranean Sea
BARTLETT	—	—	60	9	1		sideways downside ship	South Atlantic
(BACKUS et al.)		10	100	6				(NW Atlantic)
BEN YAMI et al.	—	30	75	2,5–5				Red Sea Mediterranean
SAMEOTO	—	—	40	8–11				NW Atlantic
ELLIOT		7	48	0			No ship involved	Fresh water river

Thus, the nets were later towed in pairs: either in the combination top net/lower net, or top net/middle net. For most catches, the bag-shaped Nylon net had a mesh size of 300 μ and a length of 3.80 m (MOnyl monofilament 3XX, mesh No. 4; it had 26 meshes to the centimeter, and an active filter area of 51%. Each side of a rectangle measured about 300 μ).

The total of mesh openings of this net-bag was 21 times larger than the completely submerged mouth opening. Only during the plateau cruises in 1967 was it temporarily necessary (cf. p. 22), after these nets were worn out, to continue the work with short bag nets (1.34 m) having a mesh size of 500 μ.

The net combinations used at individual stations are shown in Table 3.

For the investigation of the upwelling waters off Mauretania, the 1967 neuston glider was altered in 1968. The most important changes were: the skis now formed hollow floats, and there were two alternatives for the depth-adjustment of the net pairs. During the entire journey, work was performed simultaneously at the depths of 0-15 cm and 23-38 cm.

The neuston gliders used by the "Meteor" in 1967 and 1968 distinguished themselves by high net speed, utilization of two simultaneously operating nets, but also by small mouth openings of the latter.

In addition, a Helgoland larvae net (ø 143 cm, 500 μ) with alternating bucket mechanism (KINZER und HEMPEL 1970, not seen by author) was used on the "Meteor" in 1967. The towing speed of the Helgoland larvae net was 0.5-1 m/sec. The advantage of this type — as compared with the p. 6
conventional, vertically fishing bag net — lies in its feature of fishing several layers almost simultaneously, whereby each one is immediately adjacent to the next level. On the other hand, it has the disadvantage that organisms from all the layers are being led through the same net bag so that organisms hanging in the mesh, or those actively swimming in opposite direction can, uncontrolled, escape upwards (oral communication after "Meteor" journey 1970).

2.2 Methods

The bulk of material on which this work is based has been collected during the "Atlantic Plateau Cruises 1967" of the research vessel "Meteor" by HEMPEL and the author. The station logs "Meteor"—1967 have been published by KINZER & HEMPEL, the station log "Meteor"—1968 is added here as an appendix. Samples V-1 to V-32, and V-79 to V-81 were obtained by towing the sampling device with (and abaft) the commuter boat of the "Meteor". These catches, despite the slower and inconstant towing speed, resulted in comparable values, as established by a t-test on material obtained in Spring 1967 from the Great Meteor Seamount (HARTMANN 1969a).

On the "Meteor", the neuston nets were generally towed by a boom and, with the help of an asymmetrical bridle, they were made to run appr. 10 m away, abeam the ship's quarterdeck In this position, the net operated in relatively undisturbed waters. In 1968, it was also tried to operate the neuston glider when it was paid out appr. 80 m abaft ship The asymmetrical bridle then steered the device toward starboard into undisturbed waters. This is the optimal position when sea conditions are not too rough since, in this manner, the net operates still farther away from the ship's lights and propeller noises.

Whenever possible, the net was towed at a speed of 6 knots. A speed of more than 7 knots resulted in apparently poorer catches, perhaps because the glider would then frequently jump into the air over the trough of waves. Speeds between 3 1/2 and 7 knots brought satisfactory results.

There were considerable fluctuations in the actual speed of the sampling device (in contrast to the speed of the vessel). If a wave, coming from astern, overtook the net, the neuston glider would — in relation to the water body — move backward, while a subsequent jolt of the hawser would tear the apparatus again in forward direction at a speed of more than 6 knots.

An individual towing-time of half an hour proved to be the most favorable, since longer duration increased the risk of getting the entire length of the net-bag filled, almost to the point of watertightness, with oil, jelly-fish, protozoa, cuttlefish eggs, and algae fragments. Some catches were so much intermingled with fuel residue that only fishes could be utilized while the entire rest had to be discarded.

At a speed of 6 knots, the top net fished within half an hour theoretically an area of appr. 1,600 m^2. The lower and middle nets each filtered within the same time a water body of about 250m^3, providing the water was able to pass the nets without blockage. A flowmeter was not used[1] but the length of fishes caught indicated a through-flow at high speed. The following fishes with a total length of more than 79 mm were among the catches: 61 Scomberesox saurus (up to 136 mm), 29 Belone belone (up to 370 mm total length minus length of snout), 11 Symbolophorus veranyi (up to 125 mm), 4 Myctophum nitidulum (up to 87 mm) and 4 Myctophum punctatum (up to 91 mm), as well as 1 each of Exocoetidae (165 mm), Bathystomias gigas (100 mm), and Lestidium spec. (80 cm). This listing shows that 112 fishes representing 8 species were caught whose total lengths ranged from 80 to > 370 mm. However, the fishes obtained by BEN YAMI (et al., M.S.) from the Red Sea and the Mediterranean Sea by towing their device at a maximal speed of 5 knots (Table 1) measured only up to 80 mm in length, and SAMEOTO & JAROSZYNSKI (1969) mention a maximal length of 50 mm (1 specimen with 110 mm).

1) At the Institute of Oceanography, Kiel (Germany), an apparatus has been devised in 1970 which measures the depth of submergence of the net's mouth (KRAUSE & GRAVE, unpublished).

The 300 μ mesh was selected so that fish and invertebrate plankton could be sampled simultaneously. The following sources of possible error should be mentioned:

When determining the vertical stratification, a certain degree of imprecision resulted from the vertical motions of the neuston glider due to dashing waves. When towing against the sea, the 1967 model — which was lighter than that of 1968* — was at times even pushed down under the water surface, only to jump through the air the next moment over the trough of waves. In 1967, this resulted in an estimated amplitude of variation of up to 10 cm. The top net of the model used in 1968 never left the water entirely nor was it ever pressed completely beneath the surface. Its amplitude of variation was about 5 cm. Under calm conditions, immersion of the top-net mouth was appr. 10 cm in 1967, and about 13 cm in 1968.

A possible source of error in the quantitative comparison of the microlayers is the arrangement of several nets one upon another: WINSOR & CLARKE (1940) fished in 30 m depth with three nets arranged in this fashion; much to their surprise, they found significant differences in favor of the top net which they explained with an upward escape of the plankters. Such an upward flight of the prey conveniently diminishes the area of possible attack within the cover layer to the disadvantage of a predator. Fish "stand", so to speak, "with their back to the wall" when on the surface; they may even — as many oceanic adult fish do — leave the water in the course of their flight (LEIM 1966). It is therefore quite conceivable that, as a rule, upward flight is the preferred route of escape for ichthyoneuston. In this case, it would be the lower net that chases the organisms into the top net. Adult Exocoetidae have been personally observed by the p.7

*) Translator's note: On p.4 of the original, the author stated that the 1967 model was made of heavy mohagony and therefore needed floats (here p.10). Above, he seems to make a statement to the contrary but what he probably meant to say is that, due to the floats, this model appeared lighter on the water.

author to leave the water before the net mouth, sailing about 2 m across the device. A downward flight under the surface has been observed by SCHUTZ (1956) on the fresh-water fish Esomus lineatus, by PFEIFFER (1960) on a juvenile Mugil chelo, by HARTMANN (in press) on juvenile Liza aurata and on Blennius galerita (in preparation), and by HUNTER & MITCHELL (1967) on fish swimming with driftage.

A second possible source of error which may distort the day/night ratio, and may even simulate day conditions, is the known fact that lighting conditions influence net yield. The present material offered the possibility of investigating the degree of this influence in regard to smaller fish on Scomberesox saurus of 6-29 mm total length: Among 437 fishes from 79 night hauls, and 446 fishes from 85 day samplings, there was no difference found. It is probable that the high net speed favorably affects the sampling of smaller neuston fish. However, this speed did not suffice to catch the larger animals since the 29 large Belone, collected in the course of 9 hauls, and measuring more than 79 mm, were caught exclusively at night, or during dusk/dawn, despite the fact that they inhabit the pleuston during both day and night (cf. paragraph 4.31, p.44).

A third source of error does perhaps exist in form of the "anti-cadaver-rain" (ZAITSEV 1968): Upwelling and then drifting dead fish can distort the true picture of horizontal and vertical distribution of species, and ingested dead plankton fish in the stomach of the sampled fishes leads to erroneous conclusions in regard to the digestive state of stomach contents.

A fourth source of error originates from the position of the net openings. A fish who gets into the sluice between the side boards has, at a towing speed of 6 knots, just 0.4 seconds for orientation before he reaches the height of the net's mouth. However, since the actual net speed varies between 0 to > 6 knots (cf. p. 14), the fish may — depending upon circumstances — have more time for orientation and, therefore, a chance to escape: either away from the side boards before the net opening, or away from the net's mouth. In this manner, adult exocoetids were able to fly across the mouth of the net.

The capacity of the Helgoland larvae net in relation to the time of day has been tested by BRIDGER (1956). During the night, he caught 7 times more herring larvae and 4 times more sardine larvae than during daytime; he related this result to the diminished effectiveness of the net during daytime. As a consequence of the low towing speed, the larvae net selects the slower plankters and, also for the same reason, does not catch any ichthyoneuston. These results have remained the only qualitative comparison between fishes sampled with the neuston- and those sampled with the larvae net.

The fishes caught were preserved aboard ship in a 4% buffered formalin solution. The fresh material was transferred from the draught bucket into sample bottles with the help of a "concentrator", a beaker-shaped sieve (300 μ mesh). The length of the fishes was measured, depending on the species, to the full millimeter for up to five months after the catch. The indicated length represents — with the exception of Belone belone (cf. p. 14) the total length of the formalin-preserved animal.

Some data on weather conditions at the stations were listed in the protocols on these neuston catches. In 1968, the surface temperatures of the water were measured with the help of a wooden bucket lowered over the side. During the Atlantic plateau cruises, temperature values were obtained from the day-book of the ship's weather station, and partly interpolated. In all, 6 symbols were used in the protocols to characterize the condition of the water surface. The cloud cover was always roughly estimated.

In 1967, smooth sea and calm weather prevailed while, in 1968, several hauls had to be stopped because sea motion was too strong. In these cases, not only the height of the waves but also the course of the vessel in relation to their direction were decisive factors. In this work, sea motion and cloud cover have generally not been taken into consideration because the attempt to isolate their influence from other factors did not lead to any tangible results. The metereological influences may perhaps have been concealed by stronger factors such as patchiness, diurnal fluctuations, as well as by temperature and other regional differences. However, HARDY & GUNTHER established as early as 1935 that conditions of the oceanic surface, even at force 7 winds, do not exert any influence upon the population density of the "surface" layer, and ZAITSEV (1968) observed that typical neuston organisms remain in their biotope even when waves are 3-4 m high.

3. Material sampled

The positions of all 1967 and 1968 stations are illustrated in Figs. 2-4, pp. 19-20).

The 1967 sampling areas were mostly located in a region whose oceanic surface water, due to slow vertical convection, was characterized by p. 8
high salinity, high temperatures, and food shortage. However, in 1967, two small upwelling areas were crossed at the shelf which gave themselves away by low surface temperatures (17.3^{o}—$17.6^{o}C$, in contrast to more than $18.6^{o}C$ at neighbouring stations) (Fig. 22, p. 113).

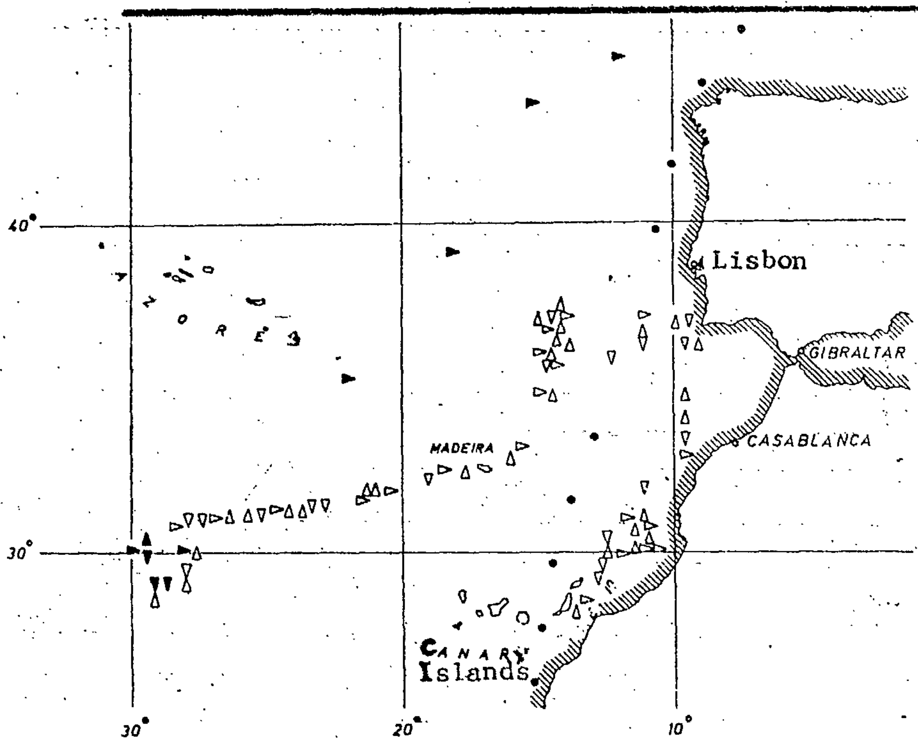


Fig. 2: 1967 stations (entire region) and northern 1968 stations. For explanation of signs cf. Fig. 4.

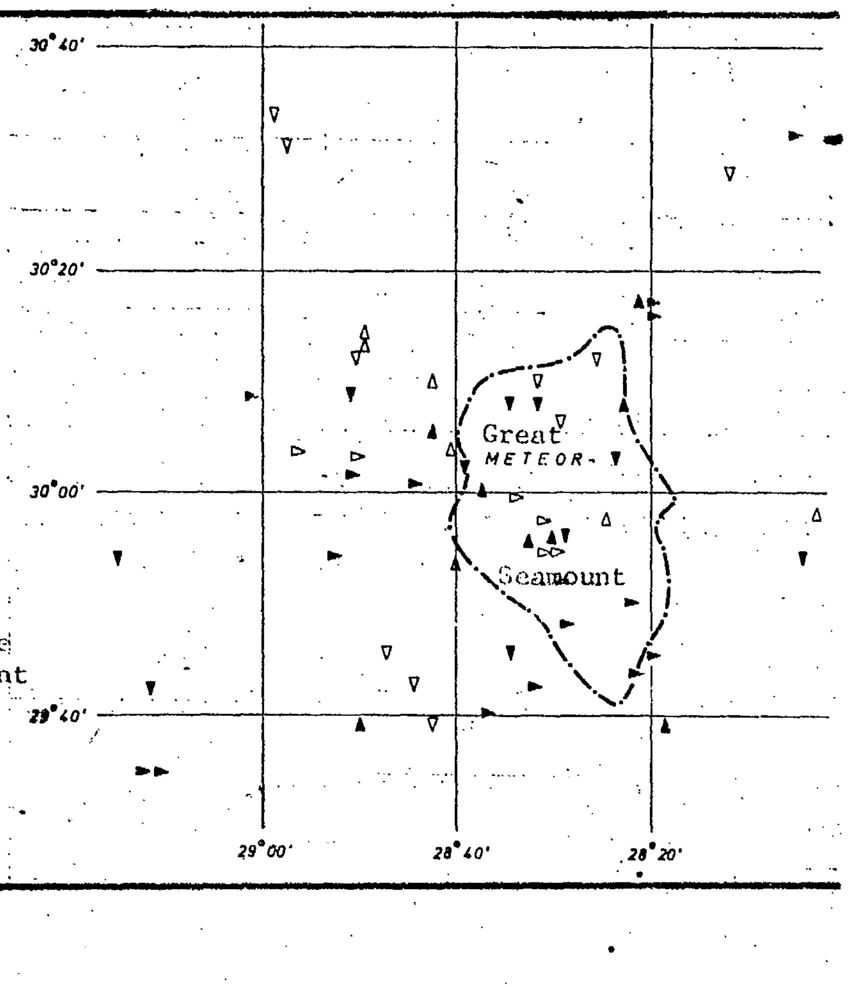


Fig. 3: Stations in the region of the Great Meteor Seamount (1967). •—•= 400 m isobath; for explanation of other signs cf. Fig. 4.

p. 9

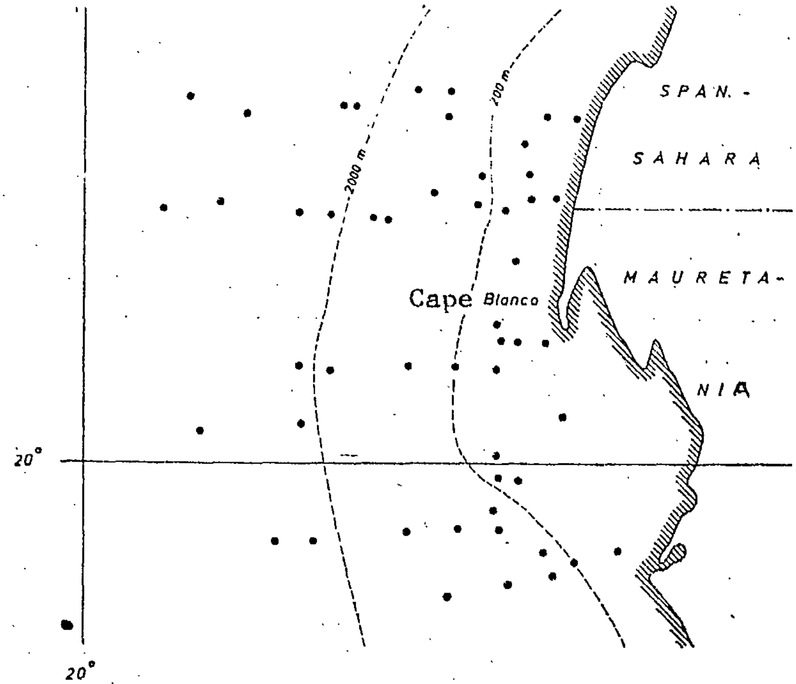


Fig. 4. Stations in the main region of investigation 1968.
Explanation of the signs:
Time of catching:
spring/day ▲
spring/dusk or dawn ▶
spring/night ▼ } 1967
summer/day △
summer/dusk or dawn ▷
summer/night ▽
● 1968

For reasons of comparison with the nutritional deficient region explored in 1967, the upwelling area off Mauretania, which is rich in food, was investigated by WEIKERT and the author in 1968 during voyage No. 13 of the "Meteor".

The regional and seasonal data on all catches are as follows:

1967:	catches	
	1-7	between English Channel and Great Meteor Seamount, from April 1st to 8th;
	8-43	Great Meteor Seamount region, from April 9th to 29th;
	V 1-V 32	at a permanent station NE of Great Meteor Seamount. from April 20th tho 26th (commuter boat);
	44-69	en route between Las Palmas and Cape St. Vincent along the African-Portuguese shelf, from June 15th to 23rd;
	70-107	en route between Portuguese shelf and Madeira, from June 23rd to July 6th;
	108-175	region west of Madeira up to Great Meteor Seamount, from July 10th to 26th;
1968:	N 1-N 11	between English Channel and upwelling region off Mauretania, from April 19th to 25th;
	N 12-N 62	upwelling area off Mauretania, from May 2nd to June 3rd.

This listing shows that samples were taken in 1967 during spring (April) and summer (June, July), but in 1968 exclusively in spring (April, May, beginning of June).

Table 2 shows, among other data, the diurnal distribution of the catches. In 1967, 70 hauls were made during daytime, 74 during dusk or dawn, and 61 during the night. In 1968, there were 30 hauls during daytime, 15 during dusk or dawn, and 17 during the night.

Table 2: Distribution of catches to time intervals

Dates	Catch		Day							SS			Night					SR
1967	Nos.	Time intervals:	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
4.4.–29.4.	3–43 V 1–V 32		10	4	4	1	3	3	3	6	8	5	1	4	3	4	4	10
15.6.–26.7.	44–69		2	2	—	1	2	4	2	2	2	—	3	1	1	1	2	1
	70–175		9	3	6	7	5	10	10	8	8	3	2	4	5	10	8	8
		Total:	21	9	10	9	10	17	15	16	18	8	6	9	9	15	14	19
1968 19.4.–3.6.	N 1–N 62		2	2	11	4	5	7	1	6	2	1	11	1	1	2	1	5

SS = sunset; SR = sunrise

For chronological comparisons of the samples taken during different seasons and at different locations, each day of sampling was divided into 16 time intervals. Sunrise (SR) and sunset (SS) were chosen as fixed points. Eight time intervals (Nos. 1-8) fell into daytime, and eight more (Nos. 9-16) fell into night. Sunrise [dawn] divided time intervals 16 and 1; sunset [dusk] fell between time intervals 8 and 9. High noon lies between time intervals 4 and 5, midnight between time intervals 12 and 13. This division into time intervals has been utilized in many of the Tables to follow. Table 2 shows the number of catches during the individual time intervals. p. 10

Series of consecutive hauls were executed especially during the dawn or dusk periods. For clearer presentation, the individual yields of these series have not been indicated in the station charts.

Which layers have been sampled at the individual stations can be seen from Table 3.

Table 3. Investigated layers

	Top net appr. 0—10 cm	Middle net 10—25 cm	Lower net 38—53 cm
1967	3— 39 41 43—148 150—168 170—175 V 1—V 27 V 29—V 32	67—148 163—164 166—167 169—175	30—65 V 1—V 32
	appr. 0—15 cm	23—38 cm	
1968	N 1—N 62	N 1—N 24 N 26—N 62	

In 1967, the top net collected 200 valid samples, the middle net 92, and the lower net 68 samples. These were complemented in 1968 with 62 top-net samples, and 61 middle-net samples. Net arrangements were changed in 1967 during the voyage: for catches 3-29 only the top net was utilized, for catches 30-65 and V 1-V 32 the lower net was added, while for catches 67-175 generally the top and middle nets were paired.

In 1968, the top/middle net-pair was used. However, of the 61 paired catches in 1968, only 45 could quantitatively be considered as double-net catches because, during the remaining catches, the lower situated middle-net bag was either damaged or blocked by algae.

With the temporarily used net, described under "Sampling devices" as being shorter (1.34 m) and having a coarser mesh (500 μ) than the neuston net-bag (3.80 m/300 μ), all 1967 commuter-boat catches were made; it was also utilized for 7 lower net catches.

The Helgoland larvae net with alternating bucket mechanism was used 27 times in 1967 in preparation for the present work: During the months of April and July at the Great Meteor Seamount, and during June at the Josephine Bank (15°W 37°N). At the Great Meteor Seamount, 11 series were sampled during daytime, and 8 during night. Of these, 5 day and 7 night series were sampled in April. In the region of the Josephine Bank there were 8 series sampled consisting of 4 day and 4 night catches.

Table 4. Some neuston fishes found in the pleustal layer of various oceans.

Authors	ZAITSEV	DAVID	PARIN	BARTLETT	HARTMANN	BACKUS et al., CRADDOCK
Location	Black Sea	Indian Ocean	Pacific Ocean	South Atlantic	Northeast Atlantic	Northwest Atlantic
Year	1968	1965a	1967	1968	1969 (a)	1969
Scomberesocidae	*	*	*		*	
Exocoetidae Myctophydae		*	*	*	*	*
Carangidae		*			*	
Clupedae		*	*		*	
Mugilidae	*				*	
Xiphias Coryphaena Nealatus			*		*	
Makaira			*	*		*
Astronesthes niger					*	*

4. Results

4.1 Listing of species

Up to now, only few results exist on ichthyoneuston of the North-Atlantic. PENNEL (1967) who studied the seasonal migration (for sampling device see Table 1) in the Gulf of St. Lawrence, found only a single species, Onos cimbrius. From the same family, the related Onos mustelus (HARTMANN 1969b), as well as herring larvae (DANIELSEN & TVEITE 1968, p. 11

HEMPEL & NELLEN 1969, among others) inhabit the pleuston of the North Sea. While, here, the number of ichthyoneuston species is apparently limited, ZAITSEV (1961) observed the bulk of pelagic eggs and larvae in the top 5 cm surface layer of the Black Sea. In the subtropical NW Atlantic, BACKUS et al. (1969) collected species which also appeared regularly among our samples: Gonichthys coccoi, Centrobranchus nigrocellatus, Myctophum nitidulum, and Astronesthes niger. In connection with this same cruise, CRADDOCK (1969) mentions in addition flying fish, sargasso fish, juvenile swordfish, sailfish, marlin, porcupine fish, tuna, and Diplophos taenia. KREFFT (private communication to NELLEN) identified the following 8 myctophydes among the yield of 9 Atlantic neuston hauls (23rd journey of R.V. Walter Herwig): Centrobranchus nigrocellatus, Gonichthys coccoi, Hygophum macrochir, Myctophum affine, Myctophum nitidulum, Myctophum asperum, Symbolophorus rufinus, and Symbolophorus veranyi. In the Gulf of Guinea, SUND & RICHARDS (1965) caught besides Auxis also five myctophyd subspecies included in the listing above. Neuston fish found in other territories are shown in Table 4 (p.23).

Table 5 lists the form or species of which our material consisted. It also shows how the individual groups were identified. Not a single specimen of the group Myctophum nitidulum could be classified with certainty as Myctophum affine.

Table 5 comprises those fish groups that were found among at least three top-net samples. According to the number of positive hauls, the highest incidence in the 262 top-net catches of 1967 and 1968 was registered for the following types: Scomberesox saurus (262 times), Gonichthys coccoi (62 times), Belone belone (40 times, Mugil spec. and Macrorhamphosus scolopax (26 times).

Table 5. List of fishes caught with top net. Type specimens were identified by MAUL and AHLSTROM.

Type or group		det. (a = according to	1967 pos. in hauls n = 200	1967 Quantity **	Total length mm	1968 pos. in hauls n = 62	1968 Quantity **	Total length mm min.	Total length mm max.
Scomberesox saurus	(WALBAUM)	a FOWLER	147	1286	6—113	15	188		136
Gonichthys coccoi	(COCCO)	MAUL	51	430	20— 61	11	167	17	
Macrorhamphosus scolopax	(L.)	a OKADA	21	56	8— 50	5	108	7	69
Exocoetus obtusirostris	(GÜNTHER)	a KOVALEVSKAJA	20	70	6— 68				
Centrobranchus nigroocellatus	(GÜNTHER)	MAUL	17	30	15— 38	1	2		
Coryphaena equiselis	(L.)	a GIBBS	17	27	10— 40				
Exocoetidae D			15	52	6— 27				
Hygophum reinhardti	(LÜTKEN)	MAUL	14	27	16— 54	3	3		57
Myctophum nitidulum	(GARMAN)	MAUL	9	20	20— 83	2	4		
Berycide		MAUL	10	10	6— 17				
Trachurus spec.		MAUL	9	27	15— 56	6	13	11	40
Myctophum punctatum	(RAFINESQUE)	MAUL	12	20	22— 91	12	114	20	
Astronesthes niger	(RICHARDSON)	a SEARS	8	8	31— 44	3	3		
Type B			8	10	11— 15				
Type C			7	68	7— 33				
Danichthys rondeletii		a HUBBS	6	8	8— 28				
Hygophum hygomi	(LÜTKEN)	MAUL	6	15	22— 70	3	9		
Symbolophorus veranyi	(MOREAU)	MAUL	6	28	18—120	5	36		125
Type D			5	8	22— 34				
Exocoetidae C			5	5	7— 28				
Nealotus tripes	(JOHNSON)	MAUL	5	5	19— 30				
Exocoetus volitans		a KOVALEVSKAJA	4	10	9— 33				
Phycis phycis	(L.)	a FOWLER	4	4	28— 49	2	3		
Cyclothone spec.			4	22					
Belone belone	(L.)	a FOWLER	4	4	23—127	36	336	8*	370*
Sternoptyx diaphana	(HERMANN)	MAUL	4	4					
Ceratoscopelus maderensis	(LOWE)	AHLSTROM	4	573	9— 18	3	69		30
Onos spec.		a D'ANCONA	3	3	26— 28	6	1074	6	42
Coryphaena hippurus	(L.)	a GIBBS	3	6	6— 33				
Exocoetidae D IIb			3	3	8— 22				
Blenniide			3	4	9— 21	11	20		30
Engraulis encrassicholus	(L.)	a FICHES	2	21					
Engraulis e. + Sardina p.	(WALBAUM)	a FICHES				27	3216	16	30
Mugil spec.						26	348	7	63
Hygophum macrochir	(GÜNTHER)	a FRASER-BRUNNER				3	5	47	70

*) Total length minus length of snout; / n = total No. of hauls;
**) calculated on the basis of standard hauls (30 min./6 knots).

The number of individuals listed in Table 5 was calculated on the basis of standard hauls at 6 knots/30 minutes

$$\left(\text{Faktor } \frac{6 \cdot 30}{t \cdot c}\right).$$

t = towing time in minutes,
c = towing time in knots.

According to the number of individuals the following are highest on the list of the "Meteor"-catches: Clupeidae larvae (3237), Scomberesox saurus (1474), Onos 1968 (1074), Ceratoscopelus maderensis (637), Gonichthys coccoi (597), Mugil spec. (348), and Belone belone (340).

The total lengths of the fishes, which will be discussed in the chapter "Ontogenetic vertical movement" (4.4, p. 52), was generally between 6 and 80 mm; however, as has been mentioned before, 112 fishes nevertheless reached lengths ranging from 80 to more than 370 mm. The majority of fishes caught in the pleustal layer were juveniles. p. 12

Some have already been characterized in the literature as "surface fish": BIGELOV & SCHROEDER (1953), among others, counted Scomberesox saurus among the most frequently found juveniles at 11° and 40° N in the Atlantic. DUNCKER (1960) reported that Belone belone stays at the surface during daytime, and Myctophidae and Astronesthes niger are known (e.g., SEARS 1964) to come to the "surface" at night. BRUUN (1935) speaks of characteristic resting position of juvenile Exocoedae at the water-air interface.

In the Atlantic samples, two families were domineering in that they represented half of the entire number from all fish groups: Next to the Myctophidae with nine, these were the Belonidae with eight groups. These as well as almost all other fishes of the collected material represent holopelagic forms. Exceptions are Onos and Phycis phycis which have barbels, as well as Macrorhamphosus scolopax if M. scolopax and M. gracilis are considered as one form (cf. 4.4, p. 55). The bottom-trawl catches made during the "Meteor" journeys contained only two forms that were caught also in the pleustal layer: Phycis phycis and Macrorhamphosus scolopax.

Comparison of the "Meteor" catches of 1967 with the groups caught farther south in 1968 showed that half of the most frequent groups of 1967 were collected again in 1968. Among the forms obtained during both journeys were 8 species of Myctophidae, and 2 each of Scomberesocidae, Macrorhamphosus scolopax, Phycis phycis, Astronesthes niger, and Engraulis encrassicholus. There were only three forms (Sardina pilchardus, Mugil spec., and Hygophum macrochir) among those present in more than two positive hauls of 1968 that had not been present also in 1967. The relative homogeneity of both the materials of 1967 and 1968 despite differing sampling conditions indicates a far-reaching area of distribution for several ichthyoneusters. As can be seen from Table 4, several families show such an extensive distribution.

4.2 Vertical distribution

4.21 Sample density

4.211 0-52 cm layer

A descriptive review on the vertical dispersion of zooplankton has been furnished by BANSE (1964). Little is known (1969) about the vertical microdistribution of metazoa on the surface.

DELLA CROCE (1962) once collected invertebrates under calm weather conditions. With one net, he consecutively sampled 10 layers which, together, covered a depth of 1 m. He attached special importance to the 40-50 cm layer because, here, the tendency toward diminishing or increasing plankton density was frequently reversed. A similar discontinuity within this layer was observed by SPECCHI (1968). However, ZAITSEV (1961) found in the Black Sea marked maxima for fish, invertebrates, and eggs already in the uppermost 5 cm layer. DAVID (1965a) reported as a preliminary result on oceanic conditions that, by day, most of the neuston is concentrated within the uppermost 10 cm layer.

Neuston stratification does, of course, vary with location and time interval, as well as according to hydrographic conditions, and with the composition of the plankton; ZAITSEV (1968) postulated varying dimensions for the layers occupied by neuston: 1-3 cm with rough sea, and 1-5 mm with calm surface waters. He observed, furthermore, that force 3 winds disturb the microdistribution of the eggs.

The 0-52 cm layer has been sampled by the author at four levels. A source of error which may possibly result from the arrangement of net openings has already been discussed under "Methods" (2.2, p.15): A maximum of organisms might be simulated in the uppermost microlayer fished by the ladder-like nets in that the nekton tries to escape preferentially by upward flight and, in this manner, does land with unrealistic frequency in the top net.

In this chapter, the amplitude of variation (estimated as up to 10 cm) will not be taken into consideration in the designation of the microlayers. In the following, the diurnal fluctuation in quantity of catches in the 0-10 cm level will first be dealt with (Figs. 5-7, pp.29-30). In Figs. 5 and 6, the thickness of the uppermost layer is estimated with 10 cm, whereas the levels beneath this layer (Fig. 6) have a thickness of 15 cm. The number of fishes per standard haul with middle and lower nets has been multiplied by 2/3 and, thus, calculated for $160m^3$. In Fig. 7, the thickness of the layer sampled in 1968 with the top net has been estimated to be 15 cm because of the deeper immersion of the apparatus then used.

ABOUSSOUAN (1965) who sampled the 0-m-level (2 knots/hr) off the West African coast, registered at the surface three times as many fish larvae ("larves") during the night than during daytime, and ZAITSEV (1961) also reports from the Black Sea that population density at the surface increased rather suddenly towards night. By contrast, FARIN (1967) found the maximum of apparent abundance during daytime. His result may perhaps p. 13 be due to the limited efficiency of the pleuston trawl which operated sideways in the lee whirls of the drifting ship and thus, presumably, collected mainly the youngest stages which, as confirmed by the results of the "Meteor" cruises, occupy the pleuston predominantly during daytime (cf. 4.35, p. 48).

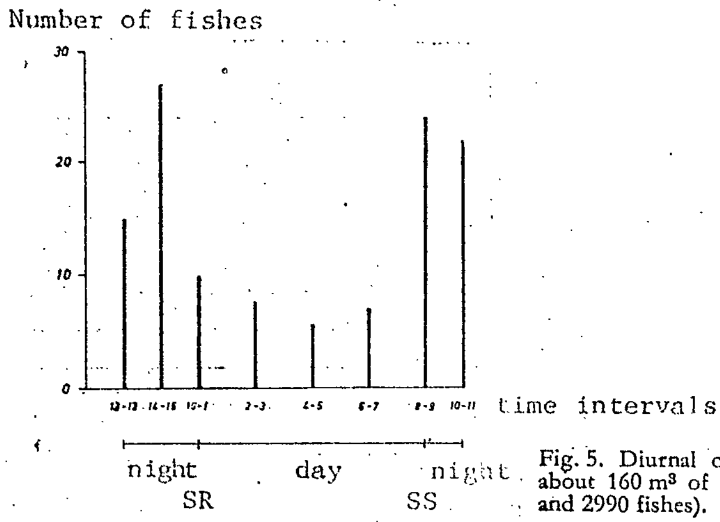


Fig. 5. Diurnal changes in number of fish caught in about 160 m³ of the 0—10 cm layer (1967). (200 hauls and 2990 fishes).

During the 1967 "Meteor" catches (n = 200), the diurnal fluctuations were surprisingly extensive as can be seen from the following figures: time intervals 16—1 = 378 fishes in 37 hauls; 2-3 = 144/19; 4-5 = 114/20; 6-7 = 220/31; 8-9 = 802/34; 10-11 = 267/12; 12-13 = 287/15; 14-15 = 777/28. The maximum after midnight (time interval 14-15) amounted therefore to 27 fishes per 160 m^3, and the minimum at noon to 6 fishes per 160 m^3. This results in a ratio of 5:1 for the extreme values. During nights (time intervals 10-15), the values were, with an average of 23 animals, three times higher than during daytime (time intervals 2-7). Comparison of yields during dusk and dawn shows that during sunset (time interval 8-9) about twice as many animals were staying at the surface than during sunrise (time interval 16-1), namely 24 as compared to 10 animals. Around midnight (time interval 12-13) a night minimum was established with 15 animals per 160 m^3.

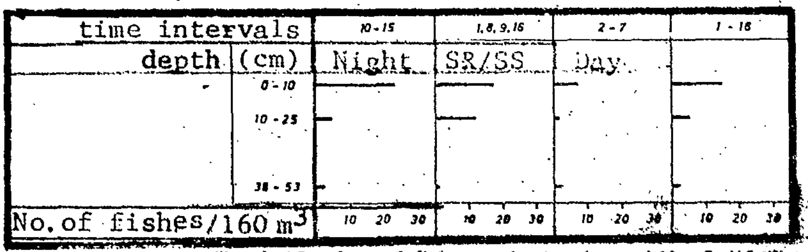


Fig. 6. Number of fish caught in about 160 m³ (1967). 200 hauls.

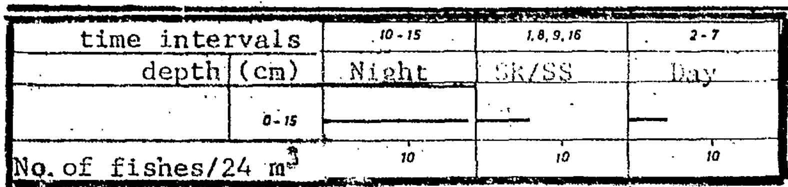


Fig. 7. Number of fish caught in about 24 m³ (1968). 51 hauls.

In 1968 (Fig. 7), as in 1967 (Fig. 6), the maximum of fish was caught in the 0-15 cm layer during the night, the minimum during daytime. The day/dusk-dawn/night ratio for 1967 (n = 200) was about 3/2,5/1, and for 1968 (n = 62) about 4/1,5/1.

The increased abundance during the night originates from the well-known phenomenon of vertical plankton migration whose causes need not to be discussed here. The minima (noon and midnight declines) illustrated above are also known manifestations of vertical migration.

The difference between the yields during dusk and dawn (time intervals 16-1 and 8-9)[2] is remarkable. The same asymmetry as well as a tendency towards corresponding diurnal migration is shown also by the precipitative volume of invertebrate plankton among these neuston samples

2) For darkness-active birds applies, according to ASCHOFF & WEVER (1962), the rule that there is more light evenings at the start of activity than in the morning when activity ceases.

(WEIKERT, oral communication). WEIKERT intends to investigate to what extent the diurnal migration of individual fish forms are synchronous with that of their principal prey. A relationship between diurnal migration of the specialist feeder *Centrobranchus nigrocellatus*, and two mollusks among this material has been observed by HARTMANN & WEIKERT (1969).

Following next, the microlayers (0-10 cm; 10-25 cm; 38-53 cm) sampled in 1967 are to be compared with one another (Fig. 6). The 1968 material did not suffice for this purpose because 16 of the 61 lower-net samples were quantitatively not valid.

Fig 6. is based on the following figures: At the 0-10 cm level, 1331 fishes were caught during 59 hauls at time intervals 10-15; 71 hauls during time intervals 16-1 and 8-9 yielded 1181 fishes, time intervals 2-7 brought 478 fishes with 70 hauls, and time intervals 1-16 nettet 2990 fishes from 200 hauls. The 10-25 cm level brought the following results: Time intervals 10-15 = 175 fishes with 30 hauls; time intervals 16-1 and 8-9 = 477 fishes with 34 hauls; and time intervals 1-16 = 695 fishes with 91 hauls. The 38-53 cm level netted: During time intervals 10-15 = 68 fishes with 19 hauls; time intervals 16-1 and 8-9 = 30 fishes with 26 hauls; p. 1
time intervals 2-7 = 56 fishes with 22 hauls; and time intervals 1-16 = 154 fishes with 67 hauls.

In summary, the yield ratios for the three levels (0-10 cm, 10-25 cm, and 38-53 cm) sampled in 1967 were: during nights (time intervals 10-15) 12/2/1; during dusk/dawn (time intervals 16-1 and 8-9) 17/12/1; during daytime (time intervals 2-7) 4/1/1, and during the entire day (time intervals 1-16) 10/3/1.

According to these figures, the apparent abundance in the three microlayers markedly decreased with advancing depth. The differences are less pronounced during daytime than during the night. The fact that the yield from the 0-10 cm level is three times higher than that of the next lower level (10-25 cm) emphasizes the quantitative characteristics of the pleuston. Fig. 9 will demonstrate also the special quality of the fishes from the 0-10 cm level (p.40).

The tendency towards poorer catches with advancing depth is indicated also in ZAITSEV's (1961) diagrams from the Black Sea.

It may have diverse causes that the maximum of plankton is found at the surface. On the one hand, the lower nets may "chase" the fish into the top net (cf. pp. 15 and 28); on the other hand, organisms of low specific gravity accumulate passively at the surface. However, generally it can be assumed that ichthyoneuston actively approaches the surface. The accumulation in the pleuston may be due to the pile-up of ascending nekton at the water-air interface, but light-conditions in the pleustal zone are probably an additional attraction for ichthyoneuston (cf. 4.7, p. 121).

4.212 <u>0-200 m stratum</u>

DECHNIK & SININKOVA (1964) studied from 1958 to 1960 the vertical distribution of pelagic fish larvae in the Mediterranean Sea. They found the maximum to be located in the uppermost 25 m of the 0-200 m stratum, and a decline in the density of their samples with advancing depth.

The result of DECHNIK (1964) from the Mediterranean Sea does essentially correspond with our findings in the 0-200 m stratum of the Atlantic in regard to the vertical dispersion of fish larvae.

During the Atlantic plateau cruises, a larvae net was utilized (cf. 2.1, p.12) which fished 6 levels (0-30 m, 30-60 m, 60 -90 m, 90-120 m, 120-150 m, and 150-200 m) almost simultaneously. The macrostratification of the upper pelagic biotope was included in the investigations for comparison with yields from the 0-10 cm microlayer (cf. 4.213, p.35), and in order to gain knowledge of the ontogenetic vertical movements (cf. 4.4, p. 52).

Before comparing the larvae-net catches with the neuston samples, the macrostratification of the upper pelagic biotope (0-200 m) shall be described separately for fish (without egg stages) and for fish eggs, as it presented itself from the larvae-net catches. The total result from the 27 runs (Josephine Bank 15°W 37°N; Great Meteor Seamount) is illustrated in Fig. 8, which is a comparison between 15 day and 12 night-series. However, since the July catches consisted almost exclusively of especially rich day-catches (6 day and 1 night runs) which distort the overall picture, the results of the series sampled in April and June have also been described separately (HARTMANN 1969a). As additional sources of error should be mentioned: Plankton accumulation in the cover layer may be simulated by way of drifting of the sampling device which becomes more pronounced towards the top. During the larvae-net operations described here, visible drifting was compensated by active maneuvers of the ship. Furthermore, the plankters clinging to the mesh and being rinsed, aboard ship, into the bucket that contains the 0-30 m catch, could very well originate from lower layers; in the same manner, the top-net sample may be enriched with fishes that manage to resist the water current in the net-bag. However, such a decisive falsification of our catch is unlikely in view of the fact that DECHNIK & SININKOVA (1964) found, in horizontal hauls, a similar vertical stratification as described hereafter. On the other hand, it is possible that more nekton successfully avoids the larvae net in this zone which is more strongly penetrated by light.

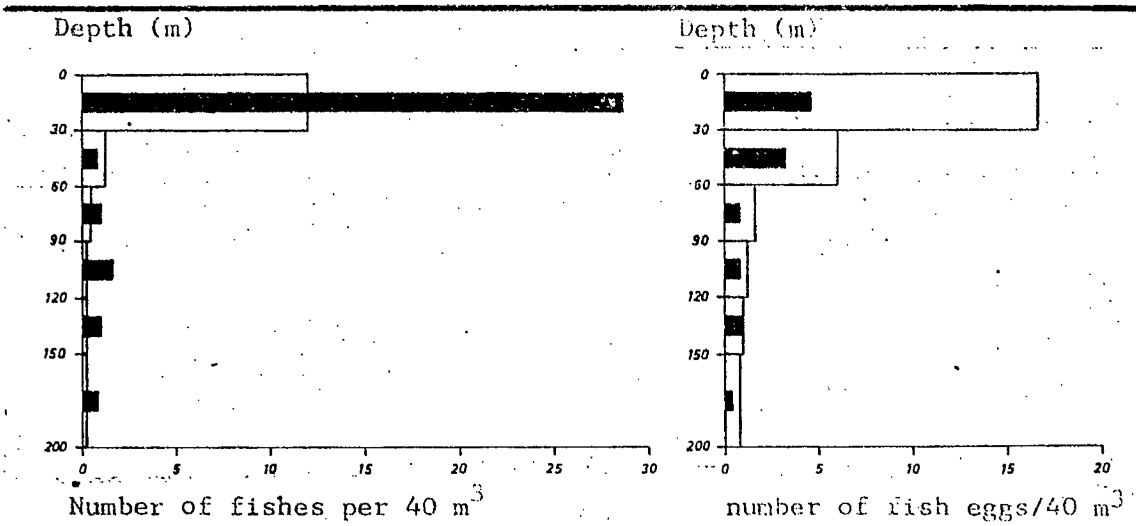
As shown in Fig. 8, the distribution of fish and eggs does show a maximum in the uppermost level (0-30 m), and there was an especially marked diminution of the number of eggs and fish with advancing depth during daytime: While, in the 0-30 m layer, an average of 16 eggs and 11 fishes per 40 m^3 were found during the day, only one egg and practically not a single fish was caught at a depth of 150-200 m. The obvious day/night difference between the egg collections in the 0-30 m layer is not significant.

At the surface, the maximum of fish (without egg stages) increased during nights. In the 0-30 m level there were two times (April, June) to three times (April, June, July) more fish (without egg stages) caught than during daytime.

In the 30-60 m layer, the number of fish (without egg stages) remained, with one fish per haul during day or night, considerably lower than in the adjacent 0-30 m top layer. The number of eggs was also lower in the 30-60 m layer, but it was still considerably higher than at the lower levels, or than the number of fish (1 fish as compared with appr. 4 eggs per haul.

As the most important result with respect to our work, the following should be emphasized: At the 0-30 m level, relatively many fishes and relatively few eggs were found whereas, at the 30-50 m level, relatively few fishes and relatively many eggs could be obtained. At the still lower levels, the ratio between eggs and fishes remained about constant. These results point towards an ontogenetic vertical movement due to which, perhaps especially from the 30-60 m level, fishes migrate into the 0-30 m level.

p. 1



White columns = day catches (n = 15)
Black columns = night catches (n = 12)

Fig. 8: Vertical distribution at 0-200 m level

4.213 Comparison: 0-10 cm/0-30 m levels

The population density in the 0-30 m macrolayer was compared with the 0-10 cm microlayer on hand of the 1967 larvae- and neuston-net samples. The larvae-net samples originated from the Great Meteor Seamount and from the Josephine Bank regions. The material available was obtained in the course of 11 daytime hauls (time intervals 2-7) and 9 night hauls (time intervals 10-15). The larvae-net catches were compared with oceanic neuston-net samples (regions 3-5 of Fig. 22; see p. 113). There were 46 day- and 36 night samples. Comparisons between the 0-30 m and the 0-10 cm levels were made by always comparing the day samples from both net types and the night samples from both net types with one another. During one haul, the larvae net fishes 40 m^3 of water (BRIDGER 1956), whereas the neuston net filters 160 m^3 per standard haul at 10 cm depth of immersion (1852 x 3 x 0.3 x 0.1); therefore, the values obtained with the neuston net were reduced to one fourth.

The mean value for day samples from the larvae-net hauls was $\tilde{x}$ = 9.3, with confidence limits (95%) at 3.9 — 14.7. For the corresponding neuston-net samples, the mean value was $\tilde{x}$ = 1.8 with confidence limits (95%) 1.24 — 2.36.

The night samples from the larvae-net hauls reached a mean value of $\tilde{x}$ = 33.4 (confidence limits 8.0 — 59.6), and those from the neuston net resulted in a mean value of $\tilde{x}$ = 4.55, with confidence limits (95%) at 2.22 — 6.88.

Therefore, the density of samples obtained (larvae net) in the 0-30 m stratum was, by day and by night, significantly higher than of those from the 0-10 cm microlayer (neuston net). This result is surprising because, in these calculations, the difference in catching-efficiency between both these nets has not even been taken into consideration. For example, the larvae net did not catch any typical neuston fish at all, due to its minimal towing speed (cf. 2.1; pp.9 and 12). The abundancies of the layers just compared could therefore differ even more strongly than indicated here. The ratio of 3.90 : 2.36 = 1.65 is statistically certain, since 3.9 represents the lower confidence limit for the mean value of the larvae-net catches during daytime, and 2.36 the upper confidence limit for the mean value calculated for the neuston-net day samples (95% confid.).

The observations made by DECHNIK in the Mediterranean Sea confirm the difference between the population density of both these layers: At the surface (0 m), the number of fishes caught is almost zero, while, at the 25 m level, they represent a maximum. This distribution of fish population is likely to depend upon the distribution of phytoplankton since, according to FRIEDRICH (1965), the maximal rate of photosynthesis throughout the open sea is usually found at a depth of 20-30 m.

The lesser number of fishes caught in the 0-10 cm microlayer as compared with the 0-30 m macrolayer is in contrast to ZAITSEV's observations from the Black Sea. ZAITSEV (1961) found, at the 0-5 cm level, fish congregations "which considerably exceeded the known concentrations." As long as no comparative catches with the same device have been made, it must be assumed that the pleustal zone of the Black Sea (0-5 cm) has a considerably higher concentration of fish than that of the investigated region in the p.16
Atlantic Ocean (0-10 cm). This could have some relationship to the particular hydrographic conditions in the Black Sea.

4.22 Vertical distribution of species

In this chapter, the distribution of types or species among the individual microlayers of the surface will be discussed.

ZAITSEV (1961) showed in a series of diagrams that larvae and juveniles of many fish types have been caught with marked frequency in the uppermost 5 cm of the Black Sea (graylings, barbels, anchovies, sea loaches, flatfishes, among others). ZAITSEV does not mention any of the types which prefer one of the four deeper microlayers within the 0-85 cm level sampled, but DANIELSEN & TVEITE (1968) who worked with ZAITSEV's PNC-5 off the Norwegian coast caught most herring larvae in the lowest (70-90 cm) of the five microlayers sampled, and SPECCHI (1968) also caught with the same apparatus in the Gulf of Trieste most eggs and larvae of Clupea and Engraulis, as well as indeterminable larvae, in one of the lower microlayers.

The following discussion of the levels does not take the undulation of the neuston net into consideration.

Table 6 and Fig. 9 illustrate the vertical dispersion of those neuston fishes that occurred most frequently among our material. First, in Table 6, the density of the catches is compared in pairs of two microlayers each, and grouped according to the types of fish. The pairs of microlayers result from the net combinations used at the individual stations: In 1967, the 0-10 cm and the 38-53 cm levels were first sampled simultaneously with two nets (top net/ lower net = t/l), and later the 0-10 cm/10-25 cm levels (top net/ middle net = t/m 1967). During the following year, the pair of top net/middle net (t/m 1968) was used simultaneously for the 0-15 cm/23-38 cm levels. The number of fishes caught with the individual combinations are listed in Table 6. Comparison of all three pairs (t/l, t/m 1967, t/m 1968) with one another does not show — as far as can be seen from the few animals caught — any essential differences between the individual combinations; therefore, the results from all three combinations have been combined in the right column of Table 6, and in Fig. 9, to allow comparison of top net/lower-situated nets (t/m or l). In this manner, the number of double catches evaluated reaches from 10 to 137, depending upon the fish type. Since, in 1967, the top net was immersed only at times, these top-net samples had to be corrected for subsequent comparison (t/m or l). The depth of immersion was estimated at 10 cm (as compared with 15 cm for middle and lower nets), and the value per standard haul was raised accordingly by half its number (Table 6). However, p. 17
even without this correction the results showed essentially the same distribution pattern for the individual species. The values from the 1968 top-net samples remained uncorrected since, then, the net worked at a greater depth of immersion (cf. 2.2; p. 15).

Table 6. Vertical distribution p. 16

	1967						1968		1967 + 1968		
	t/l		t/m		t/m or l		t/m		t/m or l		
	Quotient	n	Quotient	n	uncorrected	corrected	Quotient	n	Quotient	n	Ratio
1. Small larvae	0/42	11	27/151	19	27/193	41/193	322/10326	21	363/10519	41	1/2,8
2. Eggs	103/292	18	1384/2140	49	1387/2432	2080/2432	782/2093	21	2862/4525	88	1/1,6
3. Clupeidea larvae	21/20	3	—	—	21/20	31/20	1883/2808	26	1914/2828	29	1/1,5
4. Myctophid larvae	4/10	8	442/447	18	446/457	669/457	65/20	3	734/477	29	1/0,6
5. Hygophum reinhardti	9/13	5	18/10	9	27/23	40/23	7/5	4	47/28	18	1/0,6
6. Myctophum punctatum	8/2	3	13/6	12	21/8	31/8	112/79	12	143/87	27	1/0,6
7. Myctophum nitidulum	7/2	4	8/8	11	15/10	23/10	4/3	4	27/13	19	1/0,5
8. Exocoetidae	14/1	7	117/21	30	131/22	196/22	—	—	196/22	37	1/0,1
9. *Scomberesox saurus*	502/7	58	534/79	64	1036/86	1554/86	188/24	15	1742/110	137	1/0,1
10. *Belone belone*	2/1	2	2/1	3	4/2	6/2	216/16	27	222/18	32	1/0,1
11. *Macrorhamphosus s.*	25/1	13	—	—	25/1	37/1	107/8	4	144/9	17	1/0,1
12. *Gonichthys coccoi*	38/0	15	312/24	29	350/24	475/24	167/8	11	642/32	55	1/0,1
13. *Mugil* spec.	—	—	—	—	—	—	283/32	20	283/32	20	1/0,1
14. *Astronesthes niger*	2/0	2	5/1	5	7/1	9/1	3/0	3	12/1	10	1/0,1
15. *Centrobranchus n.*	11/0	5	14/1	7	25/1	39/1	2/0	1	41/1	13	1/0,0
16. *Coryphaena equiselis*	34/1	13	—	—	34/1	51/1	—	—	51/1	13	1/0,0

n = number of hauls
t = number of fish caught in n hauls with top net
m = number of fish caught in n hauls with middle net
l = number of fish caught in n hauls with lower net
m or l = collective number of fish in n hauls with middle and lower nets; correction (center column) and other details are explained in text.

The ratios from the right column of Table 6 (t/m or l) are graphically illustrated in Fig. 9. In evaluating the diagrams in Fig. 9, it should be kept in mind that the true distributions are obscured by the vertical undulations of the neuston glider. p. 17 cont'd

Continually migrating fish types do only slightly influence vertical stratification since, if 60 meters per hour is postulated as the speed of migrating, the fish passes, in the course of a 24-hour day, the vicinity of the lower and middle nets in 40 seconds.

On the basis of the results (Fig. 9), a surface-negative, a slightly surface-positive, and a markedly surface-positive group can be distinguished within the 0-53 cm layer.

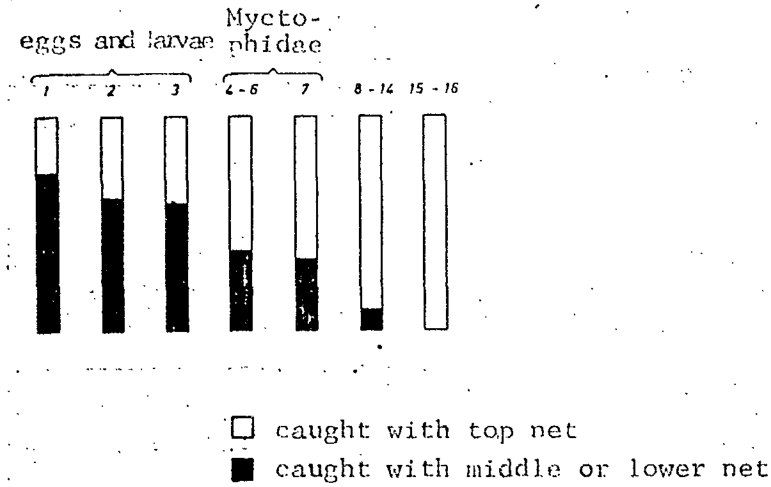


Fig. 9. Vertical distribution of species. The numbers correspond to the consecutive numbers of species in Table 6.

Individual species and stages of the fishes caught are fairly evenly distributed among these three groups.

In the following, the numerals between parentheses refer to the consecutive enumeration in Table 6 and Fig. 9. The values for the ratios (top net/ middle- or lower-net catches) are listed in the last column of Table 6.

Only the first stages of growth among our material were surface-negative: The small larvae (1), a mixture of forms that could not be classified as belonging to specific species (t/m or l, ratio 1:2,8), eggs (2) (ratio 1:1,6), and Clupeidea larvae (3) (ratio t/m or l = 1:1,5). Herring larvae investigated by DANIELSEN & TVEITE (1968) proved to be as surface-negative as the Clupeidea larvae in our material, while HARTMANN & SCHNACK (1969) observed on herring larvae in the Schlei-river (Schleswig-Holstein) also a surface-positive behavior. Finally, in our sense partly surface-negative (Osmerus eperlanus and Percidae) and partly surface-positive (Cyprinidae) were the fresh-water fish larvae in the Eider-river (Schleswig-Holstein, Germany) (HARTMANN & LINK, in preparation).

The preference for the lower microlayers, exhibited only by the first stages of growth, is presumably due to the marked ultraviolet radiation throughout the pleustal domain, as strong radiation may harm especially eggs (BREDER 1962, MARINARO 1966) and larvae (DANNEVIG & SIVERTSEN 1933). However, eggs are known to float up to the covering layer when the sea is calm.

In contrast to the conditions illustrated in Fig. 9 found ZAITSEV (1961) an especially "characteristic" abundance of fish eggs in the uppermost 5 cm of the Black Sea, which persisted even with waves up to 2 m high.

The discrepancy between ZAITSEV's result from the Black Sea and that described here in regard to vertical distribution of eggs at the surface may perhaps find its explanation in another observation by ZAITSEV (1968) according to which waves, caused by force 3 winds or more, destroy the stratification of the eggs and even kill part of them. ZAITSEV has evidently collected his material under comparatively calmer weather conditions. — It would be imaginable, furthermore, that oceanic fish eggs — in adaptation to the rougher surface of the open sea — have a higher specific gravity and therefore develop preferentially in sub-pleustal layers. Similar conditions may apply for the larval stages (compare VINOGRADOV 1970).

Slightly surface-positive were, among our material, several Myctophidae: Myctophid larvae (4), Hygophum reinhardti (5), Myctophum punctatum (6), and Myctophum nitidulum (7). For all of these, the ratios (t/m or l) were 1/0,6 or 1/0,7*. Markedly surface-positive were the remaining 9 of the 16 groups investigated; Myctophidae and other species (ratios 1/0,1 or 1/0,0); Exocoetidae (8), Scomberesox saurus (9), Belone belone (10),

*) Translator's note: In Table 6, the ratios for this group are 1/0,6 or 1/0,5. (cf. p. 38)

Macrorhamphosus scolopax (11), Gonichthys coccoi (12), Mugil spec. (13), Astronesthes niger (14), Centrobranchus nigroocellatus (15), and Coryphaena equiselis (16).

The vertical dispersion of our myctophids is similar for related genotypes since only the small (cf. 4.7, p. 121) slender-tailed myctophids Gonichthys and Centrobranchus who are barely distinguishable by outside appearance, were "strongly surface-positive."

It should be mentioned at the outset that, as a rule, neuston fishes remain only temporarily in the pleustal domain. For most groups, a diurnal migration (cf. paragraph 4.3) and an ontogenetic vertical movement (cf. 4.4, p. 52) could be observed. In connection with the vertical distribution of species, it is interesting that the characteristic phosphate stratification of the uppermost 50 cm can be maintained even at wind forces 2-4 (Beaufort scale) (cf. 4.7, p.121). p. 18

4.3 Diurnal migration

CUSHING (1951) described on the basis of Crustacae the phenomena of vertical migration. McLAREN (1963) provided a review of the attempts made to interpret these phenomena.

The values in Table 7 refer to top-net catches (0-15 cm). The number of fishes per haul has been corrected in all instances to standard hauls of 30 min. duration at the speed of 6 knots. Double hauls that fell into the same time interval were listed only with their mean values. Numbers preceded by a zero refer to 1968 samples. Only positive hauls are recorded in the Table.

4.31 Pleuston-constant ichthyoneuston

To this group belong the smallest members of the neuston population, namely Scombersox saurus measuring 6-29 mm (HARTMANN 1970 b).

Table 7. Diurnal migration

	Night			SR	Day							SS	Night			
Time interval:	13	14	15	16	1	2	3	4	5	6	7	8	9	10	11	12
Fish type	Number of fish caught with top net															
Macrorhamphosus scolopax				1 086	3 1 2	6	2 8 05 015 01	4	1	1 1 2 01	2 3	1 3 1 1	1 7 1			
Gonichthys coccoi	24 22 5 1 4 01	1 10 2 29 27 10 1 019	3 4 5 3 34 2 8 2 016	15 1 13 1 3 4 1 1 05									3 1 2 2 15 2 4 1	3 5 55 1	1 4 10 03 02 077 03 031 02	5 4 4 10 1 3 08
Trachurus spec.	12 (12)		2 1 1 1	1 (4)										1 3		3 (2)
Berycids		1 1	1	1	1		1					1 1 1	1		1	
Astronesthes niger	1 1	1 1													1 2 01 01	1 1 1 01
Coryphaena equiselis	1	2	1*	1*	1*	1	1			1*		1* 1	2 1			
Myctophid larvae		1	10	2 11 63 8 063	1 1 1	1				1 27 01	1	21 50 1 01	140 14 1 100 1		1	

* = two positive hauls made consecutively within same time interval
() = caught with lower net
Numbers preceded by zero refer to 1968 hauls

2. Coryphaena equiselis was caught, as shown in Table 7, always in form of single specimens, but these were present in 17 hauls*. This species as well as the smallest Scomberesox saurus (6-29 mm) appeared among day (9 animals) and among night catches (10 animals). The same picture, including the noon-time decline which is indicated in Table 7, resulted from PARIN's (1967) catches in the Pacific Ocean. p.1

3. Belone belone with a length of 9-78 mm (309 animals from 38 [36?] hauls) were spread over all times of day (14 night- and 22-day hauls). Although those measuring 79-370 mm (31 animals from 9 hauls) were caught exclusively during the night, this is presumably due merely to the diminished performance of the neuston glider during daytime, since DUNCKER (1960) reported that Belone belone up to 12 cm long were present during daytime in abundance at the "surface", and adult belonids could be observed in 1968 during nights in free waters, and at noon in the harbor waters of the seaport Bathurst (W. Africa) (under clear skies) directly at the surface. — Chapter 4.7 (p. 121) deals with the diurnal migration of Belone belone within the scope of overall correlations.

4. The Berycid was, according to Table 7, absent from the pleustal domain only during the time of most intensive solar radiation. 6 animals were caught in 6 night hauls, and 5 animals were obtained with 5 hauls during daytime.

5. Mugil spec. (348 animals from 26 hauls) were found in the pleuston during the day (15 hauls) and during the night (11 hauls). It cannot be determined from the present material whether individual length groups vary in their behavior. — Liza aurata (= Mugil auratus) (about 30 mm) which were caught in the harbor of Ischia Porto, prefered the 0-25 cm level during daytime, and stayed during nights immediately below the surface of a 1.45 m deep "arena" basin (HARTMANN: Internat. Rev., in press).

6. The Clupeidea larvae, 3237 Engraulis encrassicholus and Sardina pilchardus, were collected in 13 day- and 15 night-hauls.

4.32 Night-positive neuston

1. The larger neustonic stages of Scomberesox saurus (50-113 mm) belong, in contrast to those measuring only 6-29 mm, to this group (HARTMANN 1970 b).

2. Trachurus spec. (15-56 mm) is another example of night-positive ichthyoneuston. 27 animals from 9 hauls were caught exclusively during the night (Table 7).

3. Myctophids, except for the larvae (cf. 4.33, p. 46), do of course also belong to the group of night-positive neuston fish. Gonichthys coccoi, the most frequent myctophid among our catches, was represented according to Table 7 with 597 individuals from 60 hauls during all time intervals (9-16) of the night, near the surface. Not a single Gonichthys coccoi was caught during daytime (time intervals 1-8).

The sorting of the Gonichthys coccoi from top-net samples according to age and sex, namely

1) males,
2) females,
3) juveniles in which the photophores at or below the caudal peduncle were not yet developed,

resulted, in 1967, in an "adult"/juvenile ratio of 1:5. The sex ratio was even.

4. Of the larger Exocoetus obtusirostris (32-68 mm), only one individual was caught in the pleustal domain during daytime, 4 specimens during dusk and 6 animals during the night. Analogous to this, Exocoetus, caught during nights by PARIN (1967) in the Pacific Ocean, measured in most cases more than 20 mm.

5. Of the Exocoetidae D (18-27 mm), only 6 individuals were caught: Not one animal during the day, one specimen during dusk, and 5 specimens

during the night. PARIN (1967) also observed that larger Exocoetidae (in contrast to the smaller ones, see below) did stay in the pleuston during nights.

6. Astronesthes niger (Table 7) represents a special case among the night-positive neuston fish. In 1967 and 1968, 13 animals from 12 hauls were caught exclusively during time intervals 11-14, that is, around midnight. Astronesthes niger also differs morphologically from all other neuston fish obtained during the "Meteor" cruises by the smallness of its eyes.

4.33 Dusk/dawn-positive neuston

The diurnal migration of myctophid larvae (diverse species) was observed already by PARIN (1967) in the pleustal domain of the Pacific Ocean. He found myctophid larvae almost exclusively during broad daylight, and especially numerous towards evening (18 hrs) [6 P.M.] and in the morning (8 hrs) [8 A.M.]; in addition, he noted a decline at noon.

Table 7 illustrates our results from the catches in the Atlantic Ocean; 25 hauls were spaced over 24-hour days as follows: During night (time intervals 10-15) 3 hauls with a total of 12 animals, during dusk/dawn (time intervals 16-1 and 8-9) 17 hauls with 479 animals, and during daytime (time intervals 2-7) 5 hauls with 31 animals. Table 7 thus confirms in essence PARIN's observations, but with the following limitations: The dusk-dawn maxima were considerably higher in the Atlantic, the noon-time decline much more obvious, and during daytime (time intervals 1-7) only an insignificant number of myctophid larvae was caught except for one haul.

The dusk/dawn-positive behavior of myctophid larvae was recognizable also in a series of 5 consecutive 35-minute hauls (Nos. 131-135). Because of the cloud cover, sunrise could not be directly observed. Most animals stayed during dawn within reach of the middle net. However, the dawn ascension of part of the myctophid larvae into the uppermost microlayer became visible: While darkness prevailed, not one myctophid larva was found in the top net, and only few (6) were in the middle net. At the beginning of sunrise this picture had still not changed (0/5). Later during dawn there were 63 larvae in the top net and 145 in the middle net. At the time of transition to daylight one larva still landed in the top net, while 22 were still caught by the lower net. The last haul of this series did not yield any more myctophid larvae. p. 20

4.34 Day-positive neuston

1. Macrorhamphosus scolopax (7-65 mm) was found in the pleustal zone only during daytime and during dusk/dawn: 21 positive hauls were made during the day (time intervals 1-8), and 9 hauls during the dark phases of dusk or dawn (time intervals 9 and 16). No Macrorhamphosus scolopax was caught during time intervals 10-15 (night) (Table 7, p.43).

2. Smaller Exocoetidae must also, in contrast to older stages, be included among day-positive neuston. The smallest Exocoetus obtusirostris (6-8 mm) were found during daytime with 17 animals, and two more were still caught in the pleustal domain during the light periods of dusk or dawn. The next-larger group (9-19 mm) also stayed in the pleuston during daytime (38 animals) but remained still numerous (34 animals) throughout the cover layer during the lighter half of dusk or dawn. For the following group (20-31 mm), the time of their presence in the pleustal domain was shifted still further into dusk or dawn. Exocoetus of this length numbered 5 during the day, 5 during the light periods of dusk/dawn, and 2 animals were still found at the surface during the dark part of dusk or dawn.

The younger stages of exocoetid D behaved also day-positive. The length group of 6-13 mm was represented with 28 animals during the day, with 8 animals during dusk/dawn, but not once during the night. With the next length groups, distribution was shifted gradually toward the night, as it was for Exocoetus. Exocoetids D of 14-17 mm in length were represented during the day by only 7 specimens, once during dusk/dawn and by 2 animals during the night. The day-positive behavior of smaller exocoetids was observed also by PARIN (1967).

4.35 Alternating diurnal migration of two length groups

It becomes apparent from the review on diurnal migration that most neuston fishes stay in the pleustal domain only temporarily, and then during different times of the day. The ecological importance of such a distribution may, on the one hand, lie in the fact that the accumulation of individuals at the surface is being avoided, and that, on the other hand, a certain ecological isolation of individual length groups (PARIN 1967) is being achieved in this manner, since the small stages were found in the pleuston mainly during daytime, the larger stages during the night.

The length groups of Scomberesox saurus were not completely isolated from one another because the smaller animals (6-29 mm) were present in the pleuston by day and by night, whereas the larger ones (50-113 mm) were present only during the night. Thus, Scomberesox saurus is distributed according to the rule that the younger plankton stages stay higher and do not participate in vertical migration, or at least to a lesser degree than adult plankters.

The two most frequent exocoetids, however, exhibited an alternating presence of length groups in the pleustal domain: The smallest group was present exclusively during daytime, the largest almost exclusively by night. Thereby, gradual shifting of the time of presence in the pleuston took place from length group to length group, as described above.

Finally, myctophid larvae and older myctophid stages are also staying in the pleuston at different times: The larvae during dusk/dawn, the older stages by night (Table 7, p.43).

According to PARIN (1967), Xiphias and Gemphylidae represent additional examples of the alternating presence of different length groups in the pleustal domain.

PARIN (1967) suspected that the smaller stages which stay in the pleuston exclusively by day descend into deeper levels by night to avoid larger predators among their own kind and among the Myctophidae. However, to our material, such a separation of the length groups existing in the pleuston applies, in fact, only in some respects. The smaller animals of Scomberesox saurus (6-29 mm) remain there also during the night, and the neustonic length groups of Belone belone seem to be just as little isolated from one another, as Onos cimbrius were found in the North Sea during night and during daytime. Also Clupeidea larvae (23 hauls with 3237 animals) did not seek safety in greater depths during the night.

It is obvious that particularly those species which live in the pleuston in great numbers do stay day and night in this domain: Clupeidea larvae (3237 individuals caught), Onos cimbrius (852 specimens from 22 North Sea hauls) (HARTMANN 1969 b), Mugil spec. (348 specimens caught in 26 hauls), and Belone belone (430 animals caught in 40 hauls).

By way of interpreting these data it could be postulated that species with high propagation numbers can afford to dispense with the vertical migration of their young stages that live during the day in the pleuston and are thus decimated to a higher degree by predators on the one hand but, on the other, do also save their energy by the elimination of vertical movements.

Analogous to this, species whose population numbers are low in the pleuston belong to the neuston group that leaves the pleuston by night: Macrorhamphosus scolopax, Exocoetidae, and probably also the larvae of several myctophid species (as shown in Table 7, there was only one individual each caught in 13 out of 25 positive hauls), as well as Xiphias (PARIN 1967) and Gemphylidae (PARIN 1967). According to hitherto published results, Coryphaena equiselis (Table 7, p.43) and the berycids (Table 7) are exceptions since their low-numbered populations remain in the pleustal domain by day and by night.

The relationship between diurnal migration and the abundance of individuals in the pleuston as described above lets the ecological isolation of length groups appear as an adaptation to the more or less intensive danger (depending upon the time of day) that the ichthyoneuston faces from its enemies. However, it would also be conceivable that this ecological isolation of the length groups is effected by nutritional conditions; these vary in the pleuston with the time of day and sufficient food supply for the larger groups might be available only by night, while light conditions in the pleustal might suffice only by day for the small neuston fish to see the necessarily small organisms that represent their food.

4.36 Aggregations in the pleustal domain

von WAHLERT (1963) considers the formation of schools obligatory for pelagic fish which do not represent the final link in a nutritional chain. This rule excludes first of all the day-positive neuston fishes:

The berycid was found in 11 samples; three of these catches were made in immediate succession and only one berycid was found in each of these (Fig. 7) [Table 7?].* Of Phycis phycis, only 7 individuals were found among 6 samples. Other examples of lesser density during daytime are, according to sampling results: Coryphaena equiselis, Macrorhamphosus scolopax, Type D, and Exocoetidae. Furthermore, PARIN (1967) caught by day, with the pleuston trawl, larvae and juveniles of Xiphias as well as of Gemphylidae, usually in the form of single individuals; also during the "Meteor" journey of 1967, 3 Xiphias were caught in 2 hauls, and 5 Nealotus tripes (Gemphylidae) in 4 hauls during dusk/dawn or by day. Many of the oceanic neuston fishes that roam the pleustal domain by day, obviously lead a solitary life or form only small aggregations.

By night, there were not only fish types found that live in isolation such as the berycid (Table 7, p.43) and Coryphaena equiselis (Table 7), but also those species that probably do form larger schools.

Astronesthes niger must be considered as a night-positive neuston fish that is solitary by nature. In 12 hauls there were 13 individuals caught. In contrast to Astronesthes niger, so many Scomberesox saurus, Types C, Gonichthys coccoi, and Ceratoscopelus maderensis were found during nights and the dusk/dawn periods that the existence of larger aggregations can be assumed. These aggregations may perhaps represent an adaptation to food supplies because plankton is more abundant in the pleustal domain during the night than during daytime.

As a parallel observation on cephalopoda it should be mentioned that CLARKE (1966) did not observe any shoaling behavior in the only oceanic species whose adults live near the surface during daytime: the blue

*) Translator's note: While, here, the original text refers to "Fig."7, it is Table 7 which illustrates this particular statement (cf. pp.30 and 43).

Onychia carribea, whose juvenile stages did occur also in our catches (HARTMANN 1970a) whereas, during the night, cuttlefish aggregations may possibly appear at the surface of that area (BAKER 1960).

4.4 Ontogenetic vertical movement

After showing in chapter 4.3 that many neuston fishes stay in the pleustal domain only during specific times of the day, the role of the pleuston in ontogenesis will be investigated in chapter 4.4. Ontogenetic vertical movements can be observed on invertebrates and fish: CUSHING (1951) stated that, as a rule, juveniles stay closer to the surface than adult stages. Postlarval stages of the Myctophydae for example, descend for their metamorphosis to deeper layers (TÅNING in: Faune Ichthyologique = ichthyologic fauna; pp.1929 ff.), and Macrorhamphosus scolopax leaves the pelagic domain upon reaching a length of appr. 50 mm (MOHR 1937).

In the following it shall first be discussed which stages were found in the pleustal zone. In contrast to ZAITSEV (1968) and in agreement with investigations conducted in the North Sea (NELLEN, oral communication), the observations made on the present material did not show a dominance of the earliest stages, but rather a dominance of medium stages. The pleuston-negative distribution of the first stages of these fish was visible already in Table 6 (p.39) and Fig.9 (p.40).

Quantitative comparison between the neuston-net and larvae-net samples also shows that larvae live chiefly in deeper layers: Comparison of the 0-10 cm microlayer with the 0-30 m macrolayer (cf. 4.213, p.35) resulted in a significant ratio of 1:1.65 for the sample densities. This picture is complemented by the results of DECHNIK & SININKOVA (1964) who described the vertical stratification (0-200 m) of pelagic fish larvae in the Mediterrenean Sea. They found, during all three years of investigation (1958, 1959, 1960), the maximum at the depth of 25 m, and a minimum at the surface.

Many species appeared in the pleustal realm only at a minimum length of 6 mm (Table 5, p.25): Scomberesox saurus[3], Coryphaena hippurus, Exocoetus obtusirostris, and Exocoetid D, the berycid, Onos spec. (1968), p. 22
and Onos cimbrius[4] from the North Sea (HARTMANN 1969 b). A minimum length of 7 mm was observed for myctophid larvae, Macrorhamphosus scolopax, and Mugil spec. The 6-7 minimum in length applies to many day-positive pleuston individuals; the lower limits for the length of night-positive fishes lie, at appr. 15 mm, considerably higher.

The microstratification of the surface layer, the comparison between the pleustal and pelagic domains, the macrostratification according to DECHNIK (1964), and the frequency of a minimum length of 6 mm, all point to a development of the earliest stages of neuston fish in deeper strata, and to subsequent ontogenetic vertical migration. 6 mm could be considered as the "critical" length — as the conditional prerequisite for survival in the extreme biotope (cf. 4.7, p.121).

Both the Clupeidea and the myctophid larvae represent an exception to the rule that larvae seldom stay in the pleustal domain, but both these groups are, characteristically enough, not "markedly surface-positive" (Fig.9, p.40).

---

3) The fact that 45 Scomberesox saurus (Fig.11) were caught whose total length measured 6 mm represents a correction of DUNCKER's (1960) statement that the smallest Scomberesox saurus in the cover layer have a length of 15 mm.

4) RICHARDS (1959) collected, correspondingly, with oblique hauls particularly the smaller Onos cimbrius measuring up to 5 mm.

The ontogenetic vertical migration which leads the myctophid larvae to deeper strata during metamorphosis can easily be detected in the neuston samples: The transitional forms between the negligibly pigmented larvae and the larger juveniles with the characteristic pattern of longitudinal photophores are extensively absent.

Having discussed the larvae, attention shall now be focused on the juvenile stages of the pleuston. Revealing is here the composition of length stages of Gonichthys coccoi (Fig. 10) caught with the top net.

Only 6 Gonichthys coccoi were smaller than 22 mm, but 52 animals of those caught were 22 mm long. Within the length group of 26-29 mm there belonged, on the average, only 13 animals to each millimeter-subdivision whereas, in the next-lower millimeter group, there were still 75 animals — a leap which cannot be explained solely with mortality and negative performance of the net. Half of the Gonichthys (231 of 463) belonged to the narrow margin between 22 and 25 mm. Animals of this length were juveniles; they had not yet developed the photophores on or under the caudal peduncle which are characteristic for the sexes and were clearly visible on males and females measuring 44 mm or more — an indication that the diagram reflects an ontogenetic process: At a length of 26 mm the process of maturation commences which is then completed in animals of appr. 40 mm length (In: Faune Ichthyologique, 1929).

HUNTER & MITCHELL (1967) found still more compact length-spectrums than that illustrated in Fig. 10 among juveniles accompanying drifting objects.

The length distribution of Gonichthys coccoi shall now be compared with the length composition of the most frequent species, Scomberesox saurus (HARTMANN 1970 b). The smallest stages of either species occur suddenly in great numbers, but, in contrast to Gonichthys coccoi, the number of Scombersox saurus decreases only gradually with the increasing length of the animals. Here also, departure from the biotope is probably initiated by gonadal maturation: Commencing with 63 mm length the females had immature eggs, measuring 2 mm, in their ovaries. The gonads of male animals were, at that length, also visibly developed. — Analogous to this, Macrorhamphosus scolopax migrates upon attaining a length of 50 mm at which time metamorphosis to adulthood begins (MOHR 1037). The largest Macrorhamphosus caught in 1967 (n. = 56) measured indeed exactly 50 mm. There was also one individual caught in 1968 which measured 69 mm (n = 108), but this belonged most probably to the holopelagic form Macrorhamphosus gracilis (for classification of Macrorhamphosus see p. 56). — Onos cimbrius, encountered in the North Sea (HARTMANN 1969 b), which is meropelagic just as Macrorhamphosus scolopax, appears to leave the pleustal domain at a length of appr. 43 mm, since the largest specimen caught near the surface (by MIELCK 1925) was 41 mm long, and the maximal length in 1967 (n = 825) was established to be 43 mm. Onos cimbrius is still at the juvenile stage when measuring 43 mm. — A corresponding order of length groups has been observed personally on Liza aurata in the harbor of Ischia Porto (HARTMANN; Internat. Rev., in press).

The argument that the sampling device used was simply not capable of catching the larger animals can be refuted by pointing to the results of SUND & RICHARDS (1965) who, at the extremely high towing speed of 12 knots, did not catch any larger Auxis in the pleustal domain than at a towing speed of 2 or 5 knots.

p. 22

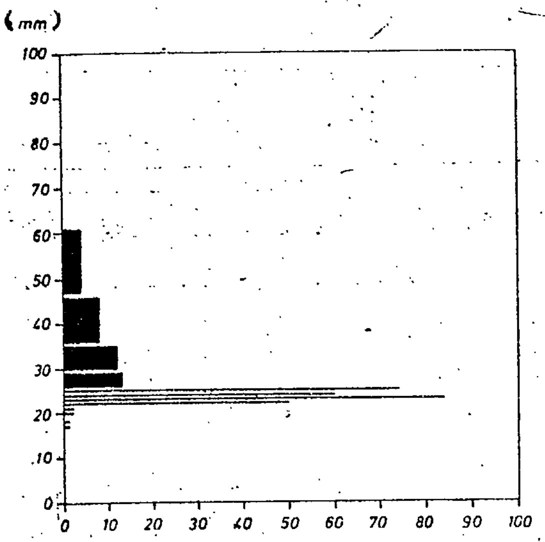


Fig. 10. Gonichthys coccoi
Frequency of length groups
(1967 and 1968).

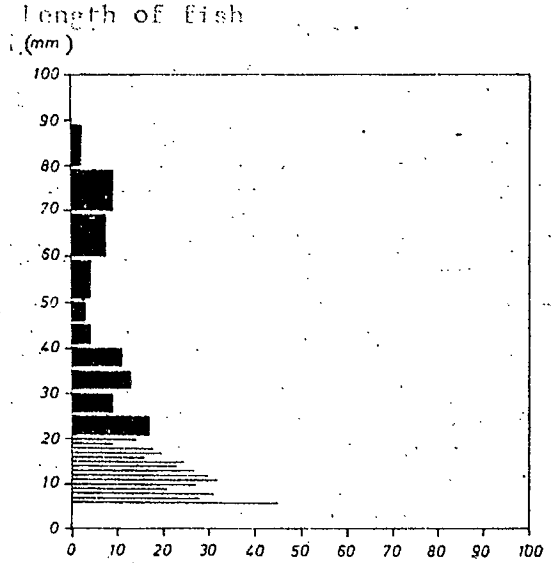


Fig. 11. Scomberesox saurus
Frequency of length groups of
those animals whose intestinal
contents were examined.

The ontogenetic vertical movements of Macrorhamphosus exhibits some interesting aspects. Before discussing these, the following facts should first be mentioned briefly: M. scolopax (L.) spends its adult life near the sea bed, M. gracilis (LOWE) in the pelagic domain. Juvenile Macrorhamphosus which exhibit all the gracilis characteristics, are species-specifically indistinguishable (MOHR 1937). OKADA & SUZUKI (1951) combined all four subspecies of Macrorhamphosus to Macrorhamphosus scolopax. — During the 1967 "Meteor" journey, M. scolopax as well as M. gracilis were caught in adult stages (colored photograph in HARTMANN 1969 a). p. 23 cont'

If scolopax and gracilis should indeed represent one and the same species, it would be conceivable that those individuals who cannot find the shelf or plateau at the time of descending from the pleustal domain, continue their pelagic existence as M.gracilis, bearing the characteristics of the pelagic juvenile forms — a parallel to the parr-markings of sea trouts that fail to migrate to the ocean.

However, if M.scolopax and M.gracilis should represent two genotypes, it could be thought — contrary to MOHR (1937) — of M.gracilis as the genetically younger species, that is, as a neotenic form of M.scolopax; this would lend support to von WAHLERT'S (1963) opinion that the population of the pelagic domain went forth from the benthos. In discussing von WAHLERT's presentation, KOSSWIG and REMANE each quoted an example of pelagic fish that could have developed through neotenic processes from littoral forms.

Adult animals, especially of the larger species, presumably do no longer cling as rigidly to the narrow pleustal domain. During the "Meteor" cruises, only few of the larger adults were observed near the surface. The nutritional requirements of many adults, further increased by propagation, can probably not be met by the pleuston alone since the amount of available food does generally decrease with each higher trophic level. The dominance of juvenile fish in the pleuston would then compose a convergency phenomenon mimicking dwarf fauna (TIMMERMANN 1932) that accompanies sargasso weed. Probably here too, the available food supply does not suffice for larger forms (TIMMERMANN 1932).

Most of the larger ichthyoneuston is, correspondingly, found only during nights in the pleustal domain, that is, at the time of maximal plankton density. It is characteristic that the only exception exists in Belone belone, that is, the species whose distribution remained limited to nutritionally rich upwelling waters (Fig.22, region 1; p.113 — Fig. 23, p.115). It should be mentioned in this connection that Onychia carrabaea whose adults — an exception among oceanic cephalopods (CLARKE 1966) — stay near the "surface" during daytime, reaches a maximal mantle length of only 36 mm.

According to our interpretation juvenile stages dominate the pleuston because — contrary to most larvae — they tolerate the physical conditions near the surface, and because for them — in contrast to the larger adults — the trophic capacity of the pleuston is still sufficient.

However, HUNTER & MITCHELL (1968) who collected fishes that accompany drifting objects with a special ring net, related in 1968 the dominance of juveniles to the natural surplus of younger stages. — From the cephalopods of our material, the adult stages were also almost entirely absent. Only Argonauta of up to 16 mm (measured from the posterior edge of the eye) carried mature eggs in their shell (HARTMANN 1970 a).

4.5 Intestinal contents

4.51 Introduction

Only a limited number of papers deals with the intestinal contents of larvae and young stages. This may be due to the difficulties involved in obtaining the necessary amount of homogeneous fish material. Here, the neuston net offers special possibilities. On account of its high towing speed, it covers a wide longitudinal spectrum and, thanks to its specialization, a narrow spectrum of species.

KÜNNE (HAGMEIER & KÜNNE 1950) compiled the results of investigations on the nutrition of boreal fish larvae. LEBOUR (1917-1933) produced five important publications on the intestinal contents of aneustonic boreal larvae and young stages. MARAK (1960) concentrated on larvae of boreal Gadidae. COVILL (1959) examined the diet of larvae and post-larval p.24

stages of boreal Ammodytes americanus. Reports on the nutrion of subtropical young stages are not known to the author.

Detailed publications on the intestinal contents of ichthyoneuston are, as yet, also not available. PARIN (1967) suspected the existence of a relationship between the vertical movements and the feeding rhythm of neuston fishes, and ZAITSEV (1970) reported that grazing takes place in the uppermost 5 cm for most pelagic fish larvae of the Black Sea. He found (1961) characteristic components of neuston in the intestines of small fishes.

In the course of numerous examinations of intestinal contents of adult fishes, diverse methods have been developed by limnologists, ichthyologists, and fishery biologists, for the evaluation and description of intestinal contents. The knowledge of earlier limnologists has been summarized by SCHIEMENZ (1922), while PILLAY (1953) supplied a more modern review.

For the present analysis of intestinal contents, a modification of the method was used which had been described by PILLAY (1953) as the "occurrence method": As the unit of measure, the percentage of fishes was utilized in whose intestines a specific type of prey was found. In this manner, the "occurrence method" is conducive to error in that prey which is frequently ingested but only in piecemeal fashion is overrated, wherea prey which is eldom ingested, but in great amounts is underrated. This error has been corrected in the present work by the vertical columns of the diagrams which take into consideration also the frequency of a particular prey in individual intestines (see below). Although the frequency of ingested organisms varies according to seasonal and regional conditions, these diagrams produced consistent results. For example, seasonal variations of ichthyoneuston showed very similar intestinal contents. These investigations were limited to the material obtained in 1967, the few exceptions are marked accordingly.

The organisms found in digestive tracts of the fish were identified according to WICKSTEAD (1965). For practical and ecological reasons, the ingested organisms were only roughly classified (HARTMANN 1969 a).

The following sources of error exist in the count of organisms found in the fish intestines, and should be taken into consideration:

1. PILLAY (1953) pointed out that objects of nutrition need varying lengths of time for passing through the alimentary canal. It is possible, for example, that too many gastropoda and too few nauplii were considered in the present material. However, since the extent of this error could not be estimated, no corresponding corrections were made.

2. MORRIS (1950) criticized the customary examinations of intestinal contents: Not everything found in the digestive tract of a fish is being digested. Particularly the easily identifiable objects could be without nutritional value for the fish as they might possibly pass the intestines undigested. The eggs of invertebrates may represent an example for such worthless intestinal contents.

Unfortunately, the neuston glider catches so gently that the more robust fish will continue to take in food while inside the net. This fact can be gathered from the fish scales found in 1967 and 1968 in almost all the larger <u>Scomberesox saurus</u> (55-113 mm); there were great numbers of them in the proximal portion of the digestive tracts.

So as to eliminate the existing error, the fresh contents from the proximal part of the intestines in 92 <u>Scomberesox saurus</u> (50-113 mm) were compared with the contents of middle and distal portions, as well as with the slightly digested food from the proximal intestines of 51 <u>Scom-</u>

beresox saurus (50-113 mm). Thus, the following percentages resulted for the individual groups of food found in the proximal and remaining intestinal portions respectively:

Calanid copepoda: 66%/66%; ostracoda: 37% each; gastropoda: 28%20%; Oncaea: 17%/10%; cladocera: 15%/35%; amphipoda: 15%/10%; Corycaeus: 13%/30%; Sapphirina: 4% each; Creseis: 1%/8%; teleostean eggs: 14%/2%.

As can be seen from this listing, extensive uniformity exists between the contents of the proximal and the remaining portions of the intestines. A marked discrepancy exists only in the case of toleostean eggs (14%/2%), but this difference is explained easily enough by the fact that the egg-remains are no longer recognizable as such in the middle and distal portions of the intestine. Therefore, in the following calculations of correlation coefficients, teleostean eggs were not included. Based on the 9 most important food groups, the correlation coefficient for the contents of the proximal and remaining intestinal portions resulted in $r = 0.87$ (95% confid. $0.98 \leqq \rho \leqq 0.59$); this value justifies the inclusion of the contents of the proximal intestinal portions — except fish scales — in the evaluation of intestinal contents from larger Scomberesox saurus (50-113 mm).

Smaller Scomberesox saurus swallowed very few scales during the day (±5%)(Fig. 12 s, p. 67), and Fig. 17 (p. 87) shows that the proximal portion of their digestive tracts is vacant by night (time interval 13-16). It is certain, therefore, that smaller Scomberesox saurus do not eat by night in the net either, and perhaps also not by day. However, it is not impossible that smaller Scomberesox saurus as well as other neuston fishes p. 25

who had no scales among their intestinal contents are capable of distinguishing between fish scales and plankton in daylight, and will therefore (— though not scales —) ingest plankton while being caught in the net-bag.

The only other species in which fish scales were also found more frequently was *Gonichthys coccoi*. 7% of the *Gonichthys coccoi* with stomach contents (1967) had swallowed scales, and in 1968 there were 8% (Fig. 14, p.77). It remains an open question to what degree earlier investigations might also have been obscured by the fact that some fish continue their food-intake while caught in the net. Despite this fallacy, the present results agree well with one another and with earlier results from the literature.

4. The last source of error to be mentioned is the "anticadaver-rain" (ZAITSEV 1968): Upwelling plankton cadavers from deeper strata, when ingested as food in the pleuston, will transmit a wrong picture of the digestive stage in which intestinal contents are found.

The results of qualitative examinations of intestinal contents are being presented in the following manner: Each Figure consists of 2 graphs, both relating to the same type of ingested organism. The horizontal columns show the percentage of fish found with the particular type of food in their digestive tracts, whereby always the number of individuals from one length group with that type of intestinal content equaled 100%. The range of each length group is also indicated in the same diagram in that the columns stretch from 1 through 5 to 10 mm fish length. The vertical columns (far right in Figs. 12a-t) illustrate the frequency with which the particular type of food was found in individual digestive tracts. The dark part of these columns shows that more than 49% of a particular length group contained more than 2 specimens of the food type indicated.

When less than 50% of the fish from this length group had more than 2 specimens of one particular food in their intestinal tract, it was indicated by a white column. This marking of the horizontal columns in black and/or white, as just explained, applies also for Figs. 13, 15, 16, and 20.

The method of preparation shall be explained on the example of Scomberesox saurus. The abdominal cavity of the fish (> 25 mm) was opened with a razor blade by a straight incision above the digestive tract. An intestinal specimen could be obtained in a very clean and speedy manner from animals of appr. 20 mm length by pulling the head of the animal carefully in frontal direction with a pincette. The intestine (with liver and gonads) then hung full length on the head, held by the pincette, and could thus be preserved under especially favorable conditions since the set of instruments otherwise used to obtain the preparation had, so far, never touched the alimentary tract. This method can occasionally be used successfully also on the smallest stages. However, small animals (< 10 mm) were usually opened under a magnifying glass with needles, and their intestinal tract was then, just as in the larger stages, slit open with a needle.

4.52 Constituents of intestinal contents

The large-scale interrelations of the individual results are presented in Fig. 20 (a-t, pp. 65-67).

4.521 Scomberesox saurus

The intestinal contents of 911 formalin-preserved animals from top-net samples were examined: 693 with positive, 218 with negative results. (The proportionate figure positive/negative is here only of limited predicative value since the amount of intestinal contents depends upon the time of day, and because only random samples were taken from large series with empty intestinal tracts.) The composition of the material by length groups is shown in Fig. 11 (p. 56): 45 animals measured 6 mm, while only 20 animals belonged to the length groups of 80-90 mm. Between the 6 mm group and the 80-90 mm group the number of animals decreased gradually.

The digestive tract of Scomberesox saurus is a tube without convolutions; there is no stomach (SCHNACKENBECK 1955). Depending upon the kind of food ingested, the rectum takes on different colorations, e.g., violet (heteropoda), brownish (cladocera), reddish (copepoda), or remains colorless. The changing coloration of the rectal portion indicates that food resorption takes place here. The food is prevented from flowing unhindered through the tube perhaps by the elasticity of the organ in vivo, and by a fold (Bauhin's valve) [valva ileocecalis] which divides the middle from the distal protion of the digestive tract.

In Scomberesox saurus a total of 19 food types were distinguishable. Fig. 12a illustrates first the distribution of "green food remains". The green residue was found only in the smallest Scomberesox saurus of 6-16 mm length, most frequently (32%) in those measuring 10 mm. Probably, these organisms are ingested more frequently than shown in the diagram, which is based only on unmistakably green coloration. Under the microscope, no outstanding structures were distinguishable. The green residue may, in part, perhaps be ingested in a secondary manner with tintinnids or mollusks, but they were also found independently from the rest of the intestinal contents.

Fig. 12b combines dinoflagellata, radiolaria, diatoms, and globigerina as "protozoa." Protozoa were found in Scomberesox saurus from the

6 mm to the 20-25 mm groups with the maximum (32%) in the 6 mm groups. This shows that they played a role only as a unit and then only in the smallest stages of Scomberesox saurus (6-8 mm), but even here were they found only in a scattered fashion among the rest of the intestinal contents.

Globigerinae were found regularly in combination with gastropoda. For example, a 15 mm long Scomberesox saurus contained nothing else besides 30 gastropoda and 1 globigerina. It could be suspected that here, the fish with an appetite for gastropoda erroneously swallowed one of the similarly built globigerinae. from p. 28

p. 26

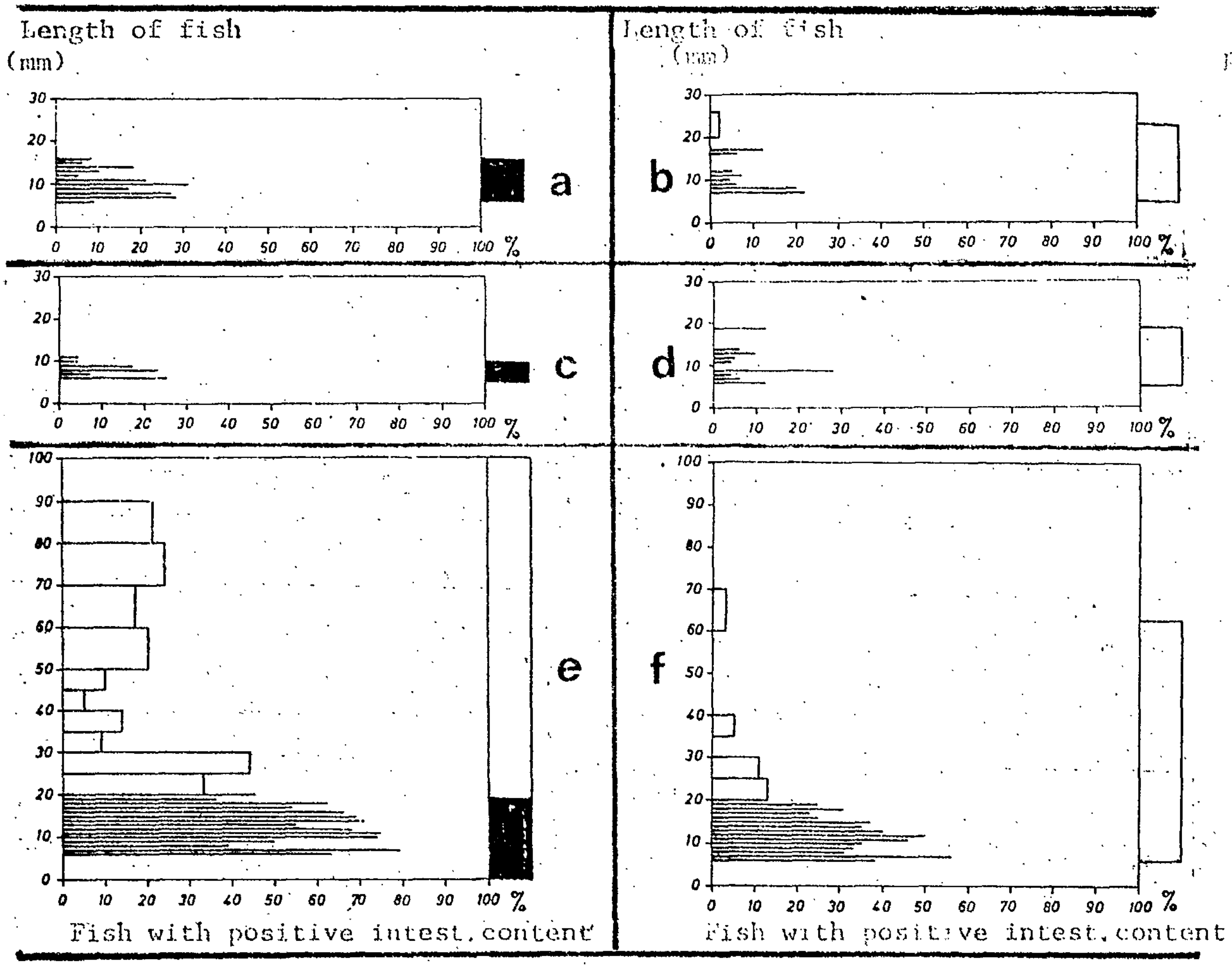
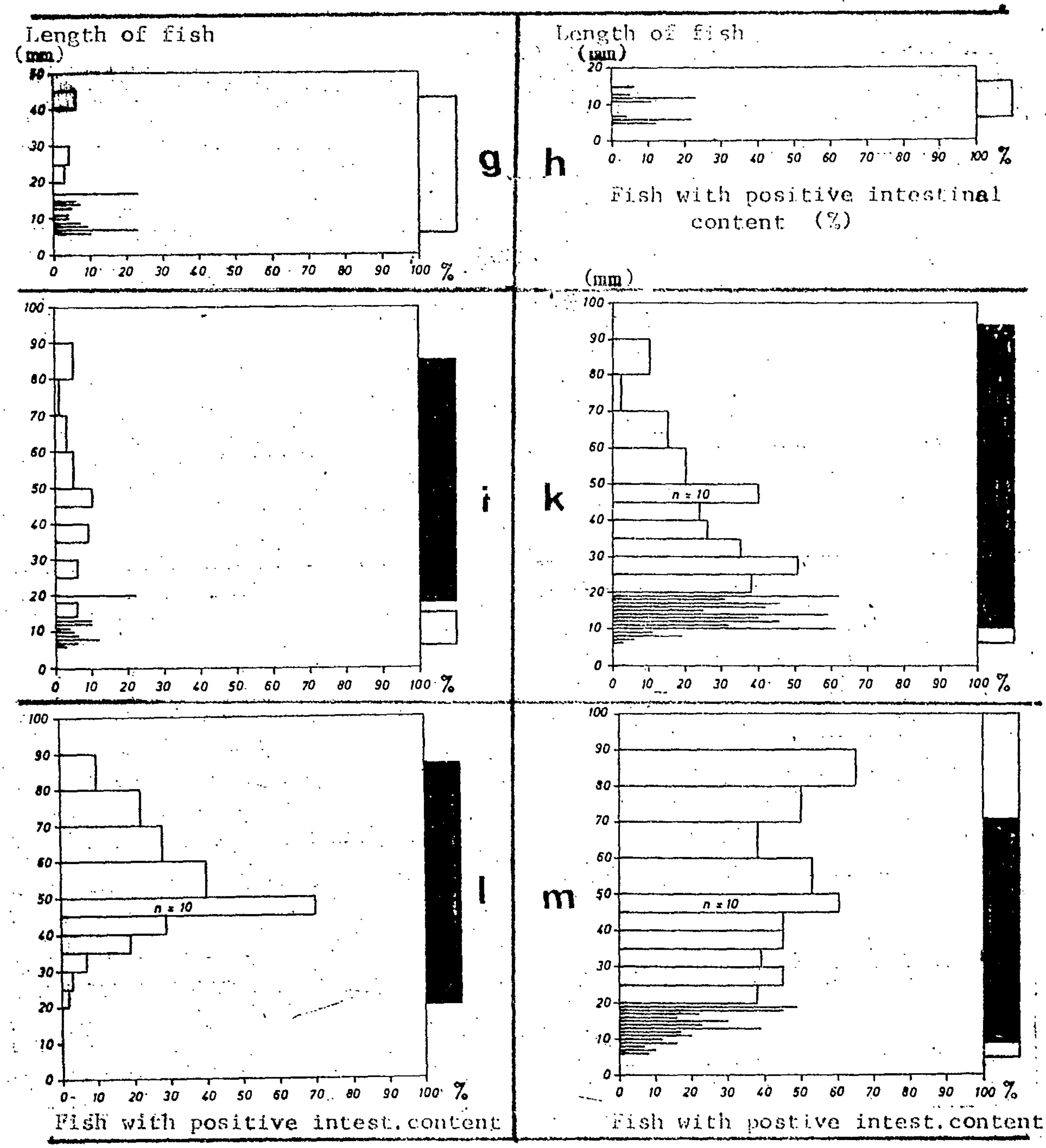


Fig. 12 (cont'd on pages 66 and 67): Intestinal contents of 693 Scomberesox saurus with filled intestinal tracts: a) green food residue; b) protozoa; c) Xystonella longicauda (?); d) Petalotricha ampulla (?); e) gastropoda without Creseis, Styliola, or Diacria; f) Creseis and Styliola subula; (p.t.o.)

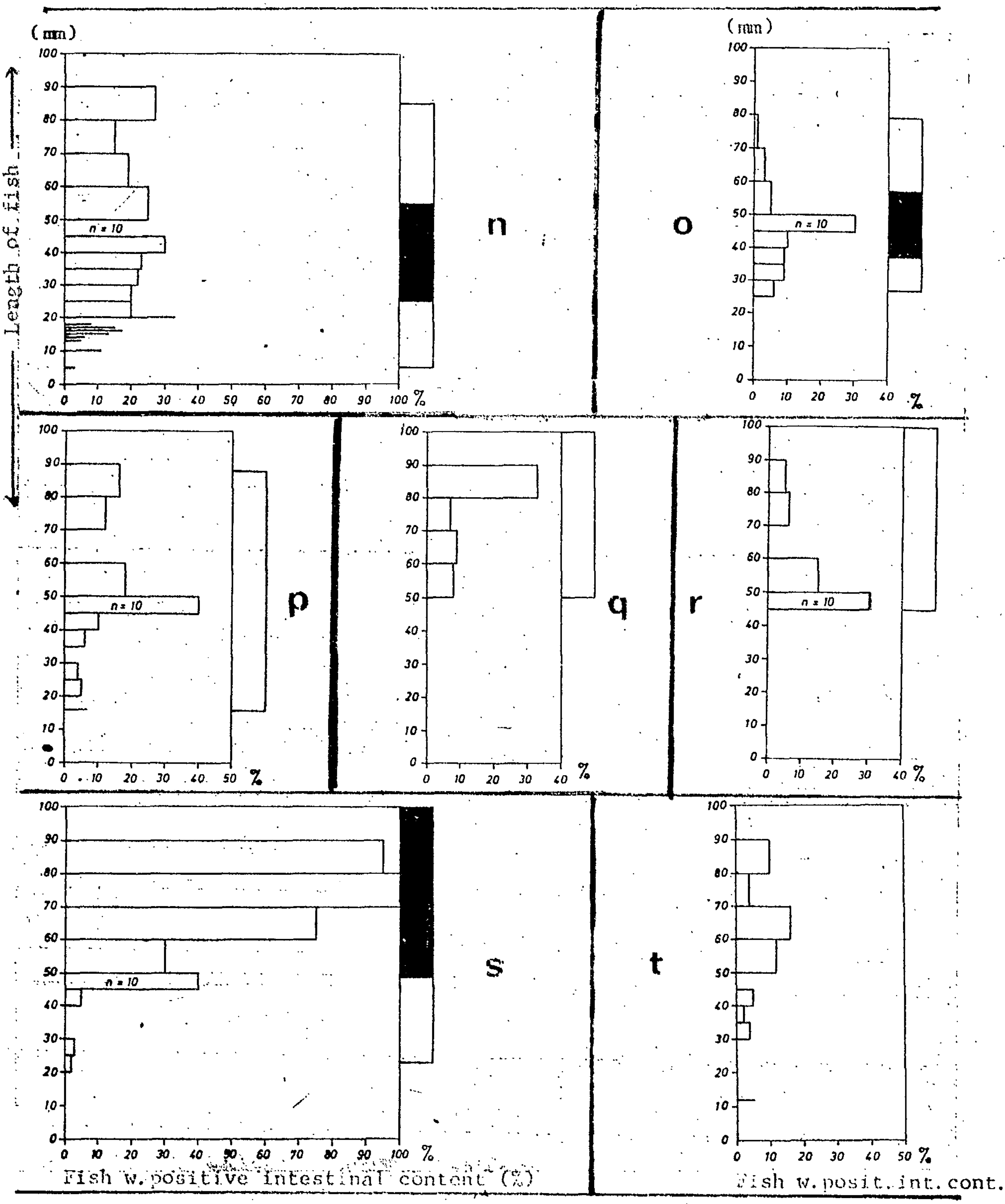


p. 27

Fig. 12 (con'd): g) Diacria; h) nauplii; i) invertebrate eggs; k) cladocera; l) ostracoda; m) calanid copepoda; (for **Fig. 12 n-t** see next page)

White horizontal columns (in Figs. 12, 13, 15, 16, and 20): $<$ 50% of the fishes had more than two specimens of the particular food contained in their intestines.

Black columns: $>$49% of the fishes had more than two specimens of the particular food in their digestive tract.



p. 28

Fig. 12 (concluded): n) Corycaeus; o) Sapphirina; p) Oncaea; q) amphipoda; r) teleostean eggs; s) fish scales; t) crumbly or pasty tar-like mass.

Translator's note: For detailed description on the design of Figs. 12 a-t, as well as Figs. 13, 15, 16, and 20, see text p. 62-63.

Globigerinae, the most frequent among the group of protoza, were found only during spring in the alimentary tract of ichthyoneuston from the Great Meteor Seamount. p.28 cont'd.

The tintinnid Xystonella (?) deserves special mention because it was ingested by the smallest Scomberesox stages only, a fact that does not apply to any other nutritional object. It was found exclusively in animals of 6-11 mm in length, most frequently (26%) in the 6 mm group (Fig. 12 c).

In the region of the Great Meteor Seamount, tintinnids were found only during the summer among intestinal contents. In some regions, these protozoa were ingested frequently and in great numbers: All 10 Scomberesox saurus (6-10 mm) from two samples contained tintinnids, partly in amounts which the protocol lists with "∞". Therefore, Xystonella (?) could play a more important role for small Scomberesox saurus than indicated in Fig. 12 c.

The second tintinnid, Petalotricha (?), was detected in appr. 10% of the fishes measuring up to 19 mm, but only in the form of single specimens (Fig. 12 d).

LEBOUR (1912-1922, p. 265) spotted tintinnids merely occasionally in boreal fish, but he believed that monocellular organisms represent a regular ingredient of the diet for Clupeidea and ammodytes measuring up to 10 mm. This length does about correspond with the values found here p.29
for Scomberesox saurus.

As for the group of gastropoda (without Creseis, Styliola subula, and Diacria (Fig. 12 e), we were dealing mainly with Atlantides. The gastropoda were, similar to the copepoda, important for all length groups of Scomberesox saurus. However, contrary to the copepoda, emphasis was placed mainly on their importance as a food for the younger Scomberesox saurus. They were found in appr. 60% of the Scomberesox saurus up to 20 mm long, and merely in 20% of the fishes measuring 50-90 mm. In the medium length groups, the gastropoda are perhaps replaced by the ostracoda (Fig. 12 l). In any case, the ostracoda diagram runs, for the middle groups, opposite to that of the gastropoda. The alimentary tract of the younger stages was often stuffed with gastropoda. For example, the intestine of one individual measuring 15 mm contained 30 shells in immediate succession.

The group Creseis and Styliola subula (Styliola s., as identified by WEIKERT according to TESCH) did occur frequently, but always in the form of single specimens (Fig. 12 f). About 40% of the fishes measuring up to 20 mm had ingested Creseis and Styliola, but for the larger stages, Creseis and Styliola remained of no importance. Similarly to Fig. 12 c, this diagram also reveals an opposite tendency to that on the ostracoda.

Among the material investigated is Diacria (Fig. 12 g) only of minor importance. Less than 10% of the fishes up to 45 mm in length contained this gastropod, and then as isolated specimens. Diacria was found only during spring among intestinal contents of fishes from the Great Meteor Seamount so that, temporarily, this gastropod attained greater importance than can be gathered from Fig. 12 g.

The presence of nauplii (Fig. 12 h) was restricted to few regions. The diagram reveals that nauplii were mostly found in singular instances and exclusively in smaller Scomberesox saurus of up to 15 mm in length; the maximum was represented by 23% of the fishes in the 12 mm group. It is possible that the nauplii play a more important part than is shown in the diagram since, especially among lumps of brown or green food residue, their delicate carapaces might easily have been overlooked. In addition, these fragile organisms should pass the alimentary tract relatively speedily so that their count, in relation to the unwieldy tintinnids and the massive gastropoda, was probably underrated.

Invertebrate eggs (Fig. 12 i) had quantitatively no significance for Scomberesox saurus. They were found in almost all length groups but in most of them merely in less than 19% of the animals, whereas, by way of comparison, 20% of aneustonic boreal Ammodytes (3-23 mm) contained invertebrate eggs (COVILL 1959). While snapped by the youngest fishes probably as free-swimming eggs, it is likely that they were ingested by the older stages together with their mother. The possible difference between indirect and direct ingestion of invertebrate eggs becomes apparent also in the vertical column of the diagram. It is also possible that the eggs of invertebrates possess no food value since, according to SCHENZ (1922), many copepoda eggs leave the alimentary tract of their predators alive, and also in our material were copopoda eggs found in the distal portion of the intestines of Scomberesox saurus that were unaffected by digestive destruction.

LEBOUR (1919-1922) mentioned invertebrate eggs in various young stages of marine fish from the boreal domain.

The maximum of the cladocera-positive fishes (Fig. 12 k) was found in the 19 mm length group (63%). Toward the 6 mm group (3%) and the 80-90 mm group (10%), the number of cladocera-postive intestines decreased gradually. Due to their mass-occurrence, the cladocera were of extreme importance to the Scomberesox saurus of medium length. Intestines that contained cladocera could be identified even by outside appearance from their plump fullness and the pigment-spots that were shining through the intestinal wall, and quite frequently the intestinal lumen was filled completely with cladocera.

The maximum of ostracoda (Fig. 12 l) was found in the 45-50 mm length group(70%). The number of ostracoda-positive intestines declined continuously toward the 80-90 mm group (10%), and the 20-24 mm group (2%). The ostracoda were important to the larger Scomberesox saurus because of the massiveness and abundance of this prey. However, for small Scomberesox saurus they seemed to be too voluminous as yet. For stretches, the gastropoda diagram takes an opposite course to that of ostracoda, which could mean that one type of food is replaced by another: While the gastropoda diagram (Fig. 12 e) shows a minimum in the 45-50 mm group and maximum values in the length groups below 20 mm, the diagram on ostrapoda shows the highest values for the length group of 45-50 mm which are diminished to zero in groups below 20 mm.

The heterogenic group of the calanid copepoda (except Pleuromamma, and without pontellids) (Fig. 12 m) was, on the whole, very important for all length groups except for the youngest stages. It is not impossible that exuviae were, in part, counted as copepoda. In any event, neuston samples contained occasionally large amounts of exuviae. The diagram shows an increase in copepoda-positive fish from the 6 mm group (8%) to the 19 mm group (40%). In larger fish, the percentage then remained constant at 50%. Fishes from 9 to 70 mm in length had, in most cases, ingested considerable amounts of copepoda (black vertical column). p. 30

Next in line are three examples of copepoda species: The pattern of the diagram for Corycaeus (Fig. 12 n) has a certain similarity to that of the calanid copepoda. It is surprising how strongly this species came to the foreground as a food for Scomberesox saurus. The vertical column shows that Corycaeus — as well as Sapphirina (Fig. 12 o) — were ingested in larger amounts by fishes of medium length. The percentage of

Corycaeus-positive fishes which was for the longer groups (20-90 mm) about 20-30%, decreased in the length groups from 10-19 mm to appr. 10%, and in the smallest *Scomberesox saurus* to almost 0%.

Sapphirina (Fig. 12 o) was limited, to an even higher degree than *Corycaeus*, to specific length groups. Just like *Corycaeus*, *Sapphirina* was also found in greater numbers especially in medium length groups (*Corycaeus*: in fishes of about 40 mm length; *Sapphirina*: in fishes of about 45 mm length). In contrast to *Corycaeus*, *Sapphirina* was no longer singled out by fishes outside the length groups of 26-80 mm.

Oncaea (Fig. 12 p) was found among intestinal contents only during spring and had therefore at that time greater significance than shown here in the diagram. Although *Oncaea* is smaller than *Sapphirina*, this copepoda-type was found more frequently in the larger *Scomberesox saurus*. This discrepancy is probably due to the diurnal migration patterns of *Oncaea* and *Sapphirina*. — In most instances, *Oncaea* was found in single specimens, and seldom in more than 20% of the animals from one length group.

Amphipoda (Fig. 12 q) were ingested only by larger *Scomberesox saurus* (50 mm and more) because of their size and probably also because their presence in the cover layer is limited mostly to the night. The intestines contained usually only single, but massive, specimens. Due to their massiveness, amphipoda have a far greater importance as fish food than shown in the diagram in which the percentages fluctuate around 10%.

The relatively voluminous teleostean eggs (Fig. 12 r) were ingestible only for larger *Scomberesox saurus*. In the present material they were of minor importance, but a discrepancy could be observed between the frequency of teleostean eggs in the proximal and the remaining portion of the alimentary canal (14%/2% in Scomberesox saurus measuring 55-113 mm). This ratio indicates that the partly decomposed teleostean eggs were no longer recognized in the distal portion of the intestines. Fish eggs are therefore of greater nutritional importance than can be seen from the diagram.

In the following paragraphs, dead matter found in the intestines as well as atypical contents will be discussed.

Fish scales (Fig. 12 s) which originated mostly from Scomberesox saurus had been digested by the majority of Scomberesox saurus measuring 50 mm or more. It can be assumed that, here, the scales lost in the net during catching procedures were swallowed by these fishes. Much like Fig. 12 s, Fig. 12 t also does indicate that Scomberesox saurus does not seem to be to choosy about its food intake: For example, fuel residue was found in appr. 10% of the animals measuring 50 mm or more. This indiscriminate intake of food could be interpreted as an adaptation to the food shortage in the biotope (cf. 4.7, p.121).

Fig. 13 summarises the preceding results on the intestinal contents of Scomberesox saurus caught in the pleustal domain. For this graph, the fish were divided into the following 4 length groups: 6-15 mm, 16-30 mm, 31-45 mm, 46-113 mm. The length of the horizontal columns indicates the percentage of fishes which contained the particular kind of food. The number of fishes from each of these length groups with either one of the identifiable intestinal contents equals 100%. Values of $< 6\%$ were not taken into consideration. The dark columns show, just as in Fig. 12, that $> 49\%$ of the fishes from that group in which a particular type of food was found, had more than 2 specimens of it in their digestive tract.

The numerical values on which this diagram is based have been tabulated in HARTMANN (1970 b). Fig. 13 illustrates that the intestinal contents in Scomberesox saurus vary with the length of the fish. According to the characteristics of intestinal contents, the following age groups can be distinguished:

1) protoza-gastropodan age;
2) gastropoda-entomostracan age;
3) entomostracan age;
4) crustacean age.

Only in the group comprising the protozoa-gastropodan age (6-15 mm) were protozoa (709%), nauplii (9%), and green food residues (16%) found among intestinal contents. The most important characteristic of this age group was the predominant role of the gastropoda (in most cases, great amounts were found in over 40% of the fishes). By contrast, Crustacea gained greater importance only among the longest animals of this group. Calanid copepoda were found to be less numerous in individual intestines (white column), and less frequent (18%) in the length group of 6-15 mm than in either of the three remaining length groups.

A parallel to these results was found in the boreal, pelagic young stages. As observed by LEBOUR (1917, 1919), young fish with the exception of the smallest stages ingested few unicellular organisms (1917); Copepoda, which were the most important food for the older stages, vanished in small post-larval stages in favor of the mollusks (1919), and mollusk larvae were, in the course of ontogenesis, often ingested before the copepoda (1917).

p. 31

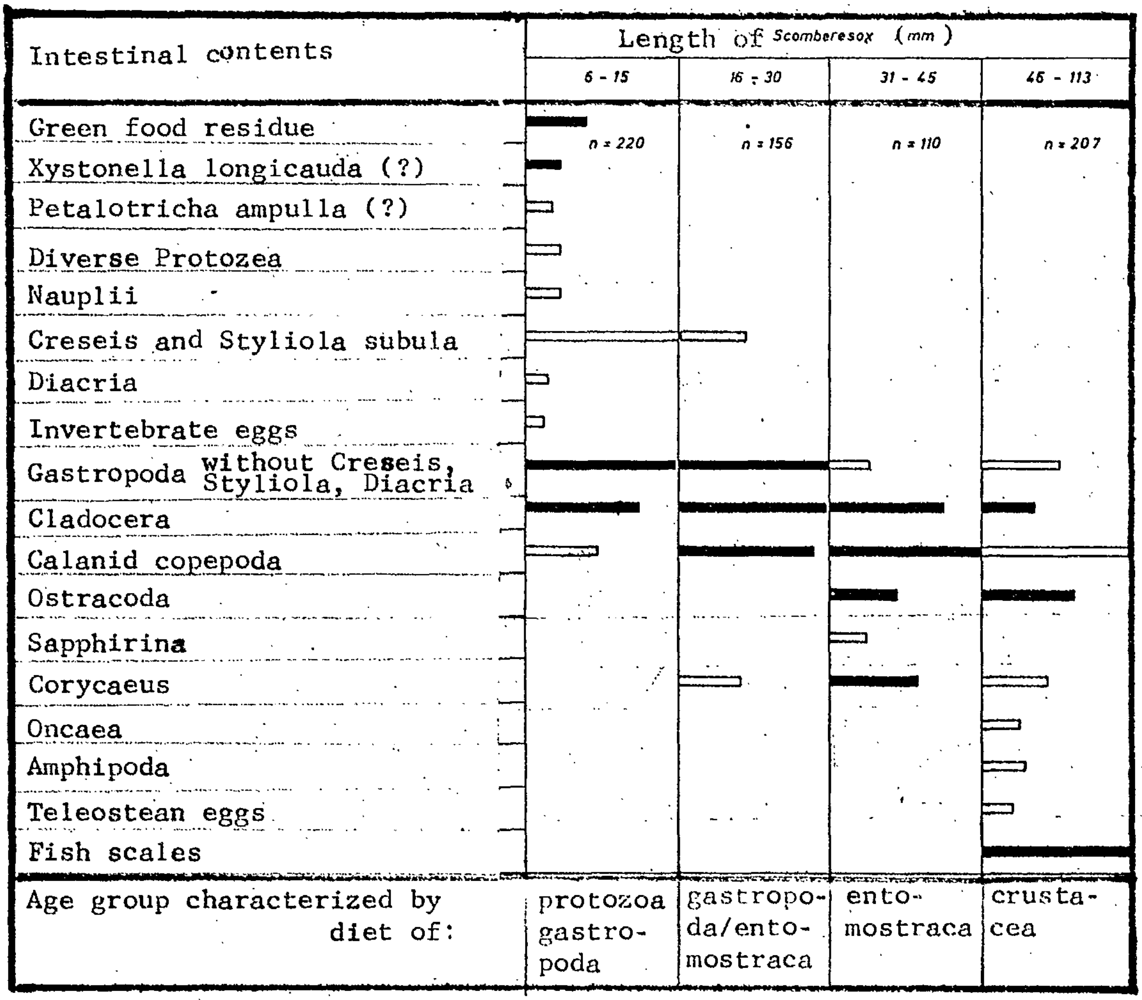


Fig. 13: Intestinal contents of Scomberesox saurus (simplified summary). For detailed description on the design of the diagram cf. Fig. 12 (p. 66) and text (p. 62-63).

0 20 >39 %
diet-positive fish

In the age group characterized by a gastropoda-entomostracan diet, (16-30 mm) many of the ingredients characteristic for the previous age group are missing from the diet: Green food residues, protozoa, nauplii, Diacria, and invertebrate eggs. Gastropoda were still ingested frequently (more than 40%) and in great numbers (black column); in addition, there were considerable amounts of cladocera (more than 40%), and calanid cope-

from p. 30

p. 31 cont'

poda (35%) (black columns). The copepod Corycaeus was found in 16% of the animals, mostly in the form of single pieces (white column). All in all, this age group ranges, according to the composition of its diet, between the previous and the following age groups.

LEBOUR (1917) repeatedly emphasized the special importance of copepoda as a nutritive for young stages. Also, her findings in regard to cladocera agree with the results illustrated in Fig. 13. She wrote that cladocera were the preferred food for young stages, and that they were ingested by the smaller stages even before the copepoda.

In the entomostracan age group (31-45 mm), the gastropoda were on the decrease (as shown by white column, only in single specimens and merely in 10% of the fishes). The cladocera retained their importance (in 30% of the fishes and mostly in large amounts), while the calanid copepoda even gained more importance (in great amounts in more than 40% of the fish). New additions were the ostracoda (usually numerous in 17% of the fishes), the cyclopean copepod Sapphirina (9%), while Corycaeus now appeared in great amounts in individual digestive tracts (23%). The intestinal contents of this age group consisted frequently mainly of entomostraca.

In contrast to both previously mentioned age groups, the fishes of the crustacean age (46-113 mm) showed no special preference for either one of their prey, which becomes visible from the white columns in the diagram. (the scales do not count since they were ingested in the net-bag). The intestinal contents of this age group showed a greater spectrum of variety than the two previous groups. New additions were massive organisms like amphipoda, diverse other malacostraca (less than 6%), as well as teleostean eggs.

4.522 Myctophidae p.32

A total of 375 Gonichthys coccoi from top-net samples (1967) were examined as to the contents of their alimentary tracts, which resulted in

262 animals = 70% with positive contents,
113 animals = 30%, contents negative.

The interesting composition of the length groups of Gonichthys coccoi is illustrated in Fig. 10 (p.56). In 1967, 61% of the Gonichthys coccoi caught with the top net belonged to the length group of 22-25 mm. None of the animals below 20 mm in length was identified, in 1967, as belonging to Gonichthys coccoi. Accordingly, the length groups from 6 to 19 mm, which were especially frequent among Scomberesox saurus, were missing from this material. This length composition exerts a visible influence upon the type of intestinal contents; e.g., smaller objects like protozoa are completely absent.

In HARTMANN (1969a), the stomach contents from 8 length groups of this myctophid are visualized in the same manner as here for Scomberesox saurus in Fig. 12 (pp.65-67). However, since fluctuations within individual diagrams did not reveal any characteristic patterns, the latter were not considered worth reproducing here. Fig. 14 summarizes the results.

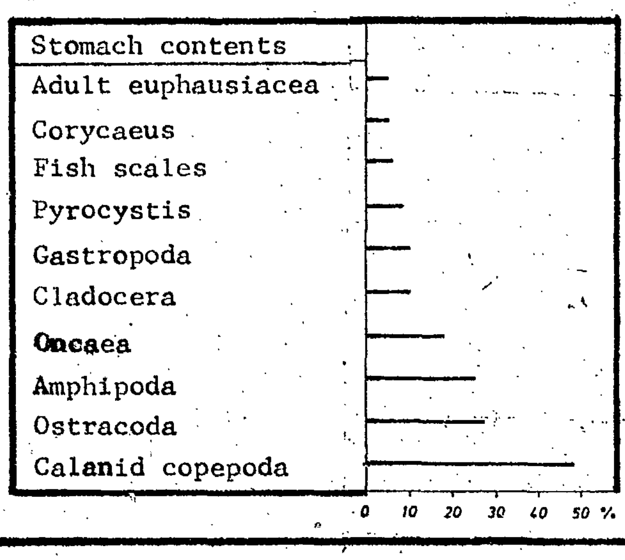


Fig. 14. *Gonichthys coccoi* / stomach content. 262 fishes with stomach content = 100%.

About half of the Gonichthys coccoi had calanid copepoda in their stomach, but in most cases only in the form of single specimens. Ostracoda with 27% remained behind the calanid copepoda. Amphipoda, which were also found mostly in single specimens were, because of their volume, more important than is shown in the diagram (26%) since a single amphipod filled the stomach of a medium-sized Gonichthys coccoi. As judged from the course of the diagram, Gonichthys coccoi enter the pleustal domain only at the time when they are big enough to ingest amphipoda. Gastropoda were ingested less frequently by the smaller Gonichthys coccoi (20-24 mm). Among the Gonichthys coccoi with stomach contents there were 9% that had ingested gastropoda. Cladocera remained of lesser importance (9%) to Gonichthys coccoi especially since only single specimens were found in the stomachs. Oncaea, found in 18% of the animals, was represented always by only a few specimens. Pyrocystis was found in especially great numbers in the stomachs of Gonichthys coccoi measuring 47-61 mm, but occurred in total only in 8% of the Gonichthys coccoi with stomach contents. Fish scales had been ingested by 6% of the Gonichthys coccoi, that is, not as frequently as by the Scomberesox saurus (Fig. 12 s, p. 67). This could mean that Gonichthys coccoi are less inclined to eat while caught in the net-bag, or that this myctophid is more choosy in the choice of his food than Scomberesox saurus. Corycaeus was found only in the medium length groups and always only as single specimen; with a total of 5%, the importance of this material remained minimal. In the night-positive Gonichthys coccoi, the various food-types were represented only by single exemplars in the majority of cases. This may perhaps be due to the fact that the plankton aggregations disperse upon nightfall and the plankton individuals are thus distributed more evenly throughout the water. The dispersion of aggregations at the surface upon darkness is a well-known phenomenon of the diurnal migration of plankton (CUSHING 1951).

The great importance of the crustacea, especially of the copepoda, becomes obvious from Fig. 14: Crustacea accounted for the five most frequent food types; calanid copepoda alone were found in 48% of the Gonichthys coccoi with stomach contents. Terrestrial insects, apparently blown to sea*) which can at times make up for half the stomach contents in Gonichthys coccoi (BRADDOCK 1969), played no role at all in our material.

The stomach contents of the myctophyds Hygophum reinhardti, Hygophum hygoni, and Symbolophorus veranyi showed a certain similarity (Table 8, p. 80): None of the animals had an empty stomach (by contrast, 30% of Gonichthys coccoi had), and a high percentage had (unidentified) remains in their stomach (37%, 80%, 68%). The percentage of calanid copepoda among stomach contents was very high (78%, 80%, 79%). (The copepoda contents in Gonichthys coccoi amounted only to 48%.) The percentage of ostracoda (22%, 27%, 14%) was higher than in Myctophum nitidulum (4%), or Myctophum punctatum (9%) (Table 8, p. 70).

The small myctophid Centrobranchus nigroocellatus turned out to be a "food specialist". His food consisted almost exlusively of mollusks (HARTMANN & WEIKERT 1969). After Centrobranchus nigroocellatus, the second of the food specialists among our neuston samples should be mentioned, p. 33
namely Macrorhamphosus scolopax (25-50 mm) who, within limits, is also selective about his food. It seems that his pipette-like mouth is especially well suited to suck up Pyrocystis. 58% (n = 36) of the larger Macro-

*) Translator's note: checked against original article by J. E. CRADDOCK (Oceanus 15:10-12, 1969)

rhamphosus scolopax (25-50 mm) had ingested Pyrocystis (Fig. 15), while this dinoflagellate could be detected only occasionally and in low numbers in the alimentary tract of other species (Gonichthys coccoi 8%, 5 myctophidae 2%).

Table 8. Stomach contents of myctophids from the pleustal domain (1967)

	H. rein.		*H. hyg.*	*M. nit.*		*M. punct.*	*S. veranyi*	*G. coccoi* %
Total number	27	(16)	15	25	(12)	13	28	375
Empty stomach	—	(—)	—	—	(2)	2	—	30
unidentified remains	10	(11)	12	17	(2)	5	19	25
calanid copepoda	21	(16)	12	8	(3)	7	22	48
amphipoda	1	(2)	3	9	(2)	1	3	26
Oncaea	4	(4)	3	8	(4)	2	2	18
Euphausiacea	3	(—)	—	4	(—)	2	6	5
gastropoda	7	(3)	2	2	(2)	1	3	10
fish scales	—	(—)	—	2	(—)	3	1	7
isopoda	—	(—)	—	1	(—)	—	—	—
Pyrocystis	—	(—)	1	1	(—)	—	—	8
zoea	—	(1)	1	1	(—)	2	1	—
ostracoda	6	(6)	4	1	(1)	1	4	28
cladocera	8	(4)	—	1	(1)	2	2	10
"tar"	—	(1)	—	—	(—)	1	—	—
Sapphirina	1	(—)	—	—	(—)	—	1	—
Miscellaneous	4	(4)	—	1	(—)	3	—	—
Number of samples	14	(7)	6	16	(11)	9	8	—

Numbers between parentheses refer to animals caught with middle or lower nets

Except for Centrobranchus nigroocellatus and Macrorhamphosus scolopax, no other food specialists were found among our material. Fig. 20 (p. 95) will show that the intestinal contents of ichthyoneuston of similar size, which had stayed in the pleustal domain at the same time, were surprisingly alike. This minor specialization, which is in contrast to LEBOUR's observations (1917-1922) on boreal pelagic young stages, could represent an adaptation to the poor food supply (cf. 4.7, p.121) in the subtropics: A fish of the plankton-poor subtropical pleuston can perhaps not afford to be choosy because the tropical plankton is very heterogenic and the specific species occur too sporadically to serve as the exclusive food. The fact that even "tar" and fish scales were ingested also points to a minor extent of specialization among our ichthyoneuston in regard to their food;

in large amounts (Figs. 12 s and t, p. 67). In harmony with our observations on fish is HERRING's characterization of the isopod Idotea metallica (driftage fauna) in the East-Atlantic as being omnivorous.

4.523 Trachurus spec.

All Trachurus spec. were caught during the night. The stomach contents of the 15 animals were the following: 12 times Oncaea, 6 times Corycaeus, 6 times ostracoda, 5 times calanid copepoda, and once mollusks. Fig. 20 (p. 95) offers a synopsis of these data in relation to the other findings.

4.524 Macrorhamphosus scolopax

In this species, which is characterized by a tube-like mouth, the entire alimentary tract was examined.

The material originated from 22 samples caught during spring (1967) and could be divided into two length groups: 8-22 mm (20 animals), and 24-50 mm (35 animals).

Fig. 15 visualizes the great importance of calanid copepoda for both length groups of Macrorhamphosus scolopax (75%, 85%). Next to the calanid copepoda are the cladocera an important food for both length groups (45%, 78%).

For the larger Macrorhamphosus, the copopod Coryçaeus played, with 85%, a surprisingly extensive role. By contrast, in the smaller Macrorhamphosus scolopax (8-22 mm) only 5% of the species Corycaeus were found. Frequent and numerous in the larger Macrorhamphosus scolopax were also Pyrocystis (58%) and the ostracoda (26%). The fact that Pyrocystis was ingested in great numbers by more than half of the larger Macrorhamphosus scolopax (24-50 mm), but not by the other species that graze in the pleustal domain during daytime (Fig. 20, p. 95), led us to believe that the ball-shaped Pyrocystis are easier gathered with the pipette-mouth of Macrorhamphosus than by the jaws of other fishes that work more like a pair of pliers.

p. 34

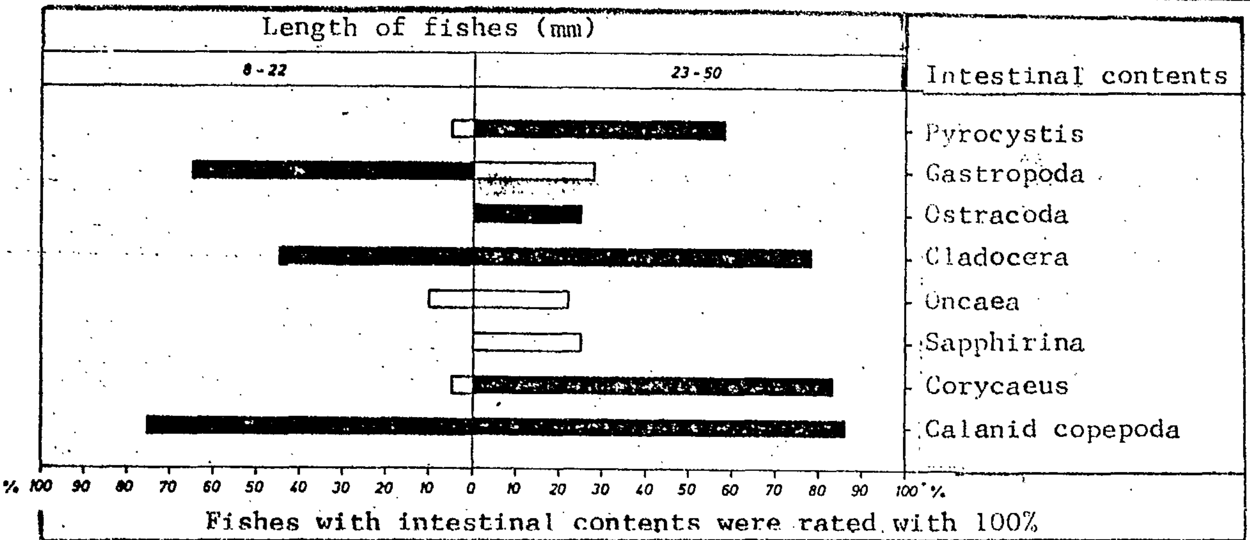


Fig. 15. Contents of the alimentary tract of Macrorhamphosus scolopax (1967). For detailed description on the design of the diagram cf. Fig. 12 (p. 66) and text (p. 62-63).

The most important food for the smaller Macrorhamphosus scolopax were, next to the calanid copepoda (75%), the gastropoda (65%). Comparison of the varieties of food ingested by both length groups (Fig. 15) shows that the smaller animals had only a limited choice of species at their disposal.

As shown by the black bars, most food types were intensively utilized by Macrorhamphosus scolopax.

4.525 Exocoetidae

1. Fig. 16 illustrates the results obtained with 77 Ecocoetus (70 E. obtusirostris and 7 E. volitans) from 18 top-net samples. Their length ranges from 6 to 33 mm. In the diagram (Fig. 16), the results are presen-

ted separately for the following 4 length groups: 6-8 mm, 9-14 mm, 15-18 mm, and 19-33 mm. As can be seen from Fig. 16, mollusks had been ingested most frequently by the smallest length group (92%), while their importance gradually decreased with increasing length of the fishes (60%, 32%, 8%). In the length group of 19-33 mm, the mollusks were found only as single specimens. The cladocera-diagram takes an opposite course to that of the mollusks: a higher percentage of cladocera-positive animals in the larger length groups and a lower percentage for the smaller length groups (76%, 84%, 60%, 18%). The same tendency becomes apparent in the copepoda-diagram (76%, 38%, 32%, 26%). In the length group between 6 and 8 mm, the copepoda were found only in single specimens. In comparison with the mollusks, cladocera, and copepoda ingested, Exocoetus had hardly touched any of the other food listed as "miscellaneous". The percentage for the latter increased with increasing length of the fishes: 0%, 10%, 12%, 18%.

The diagrams of Fig. 16 show that the small Exocoetus had ingested mainly mollusks while, with increasing length, the portion of entomostraca in the alimentary tracts grew. Mollusks, cladocera and copepoda made up the basic food for Exocoetus.

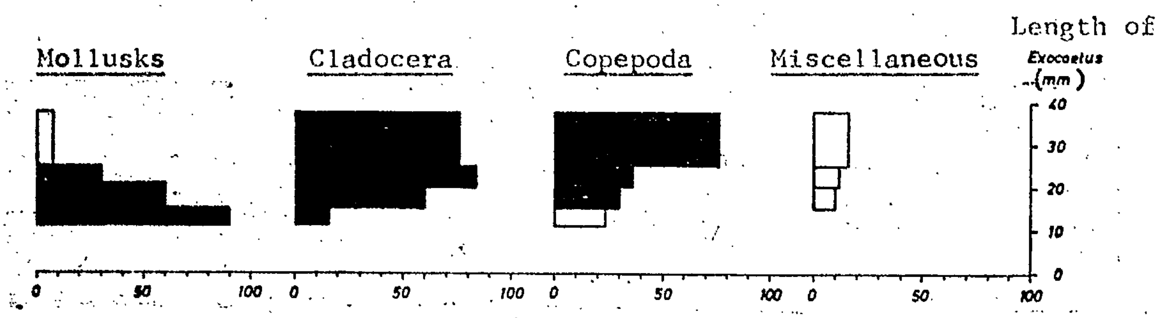


Fig. 16. Stomach contents of Exocoetus obtusirostris and Exocoetus volitans (n = 70 + 7). For detailed descripton on the design of the diagrams cf. Fig. 12 (p. 66) and text (p. 62-63).

2. Only 24 individuals of exocoetid D with a length of 6-17 mm from 11 top-net samples contained distinguishable food in their alimentary tracts. None of the animals contained fresh food, but gastropoda, cladocera, and Corycaeus (Fig. 20, p.95) pointed to a daytime grazer.

4.53 Feeding rhythms p.35

4.531 Introduction

Feeding rhythms are known phenomena in invertebrates (MARSHALL & ORR 1955) and vertebrates. SCHIEMENZ (1922) reported that fresh-water fish in plankton-rich lakes usually digest one meal completely before they will eat again — a phenomenon which was observed experimentally by MOORE (1941). LEBOUR (1919-1922) established the feeding rhythms of fish larvae and young stages. According to ZUSSER (1956) the majority of planktotrophic pelagic fish eat in the morning and again in the evening: "Planktotrophic fishes do not ingest food during the night, but they do nevertheless stay in the surface layers of the water body." A smaller proportion of the planktotrophic pelagic fish eats, according to ZUSSER, during daytime. A divergency of feeding rhythms according to the length groups of the fishes is described, e.g., by DARNELL & MEIEROTTO (1965): The younger stages of the fresh-water fish Ictalurus melas eat during dusk and dawn, whereas the adult fishes ingest their food after darkness has settled, but the exact time of food absorption could not be determined.

Unfortunately, it is not possible to determine with certainty from the feeding activity of the fishes while caught in the net (cf. 4.51, p.61-62) whether feeding activity would have been pursued by them at this particular time also under normal conditions. Therefore, in the present work, the time element of food intake was estimated mainly on the basis of the percentage of animals whose respective portions of their alimentary tract were filled to varying degrees during individual time intervals.

4.532 Pleuston-constant and day-positive neuston

The first three of the following neuston groups inhabit the pleustal domain on a permanent basis: The smallest pleustal stages of *Scomberesox saurus*, *Coryphaena equiselis*, and one berycid.

1. The feeding rhythm of the smallest *Scomberesox saurus* among our material (6-50 mm) is described by HARTMANN (1970 b): *Scomberesox saurus* measuring 6-50 mm feed during the day and discharge bowel contents during the night.

2. Of *Coryphaena equiselis* (10-40 mm), a total of 27 animals were examined; 14 of these contained identifiable food in their stomach. 12 of the 18 fishes caught during time intervals 10-1 (night), but none among the 9 fishes caught during time intervals 2-9 (day), showed an empty digestive tract. Fresh stomach contents could be established only in animals caught during the day, and in one specimen from time interval 14 (night). Especially well filled were the stomachs of animals caught during evenings. *Coryphaena equiselis* (10-40 mm) grazes during daytime, as indicated by these findings.

3. From one species of *Berycidae*, 11 individuals (6-17 mm) from 11 samples (one of these caught with the lower net) were examined. The stomachs of four berycids caught during the latter half of the night were empty. Four animals with fresh food contents originated from hauls made during dusk. Two animals caught in the morning (time intervals 16 + 1) were found to have empty stomachs. According to these results does the berycid graze during daytime, as is indicated also by the type of food identified (Fig. 20, p. 95).

The two following groups belong to the day-positive neuston group.

4. Of 56 Macrorhamphosus scolopax examined (8-50 mm), only one caught at the end of night (time interval 16) had an empty stomach. During dawn (time intervals 16-1) there was no fresh food in either of the 7 animals examined, in contrast to our findings in animals caught during daytime. According to these observations Macrorhamphosus scolopax (8-50 mm) ingests its pleustal food exclusively during the day.

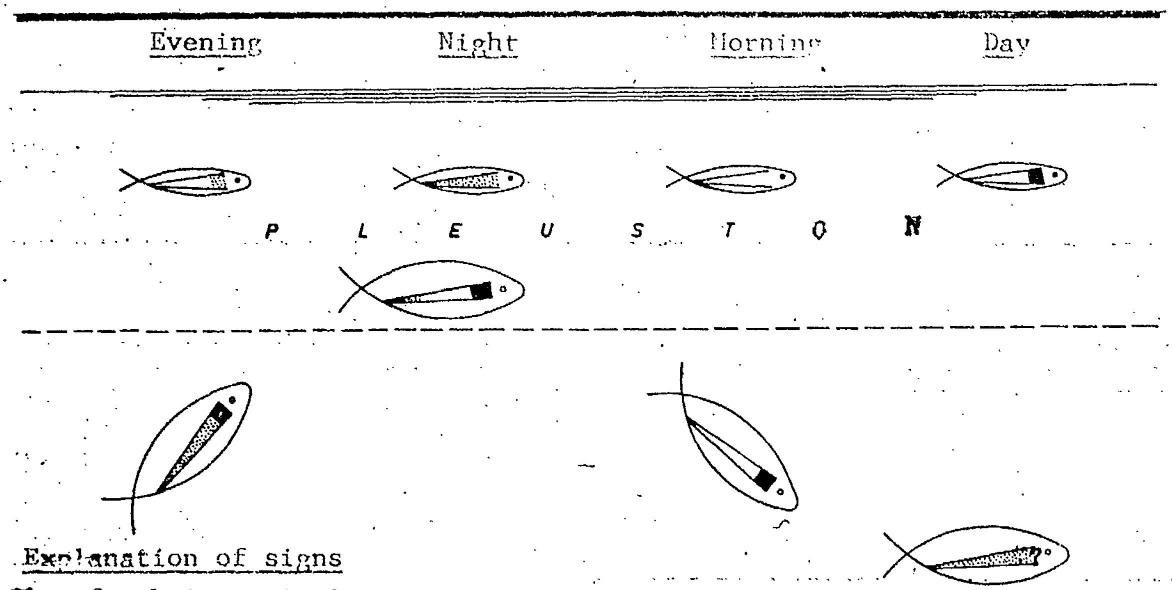
5. Of the smaller Exocoetus obtusirostris (6-17 mm), 68 animals were examined. In contrast to all 23 animals caught during the evening (time interval 8), had 6 of the 7 animals caught during dawn (time intervals 16 + 1) an empty stomach. During daytime (time intervals 2-7) the stomach contents of half the animals (17 out of 38) showed partly digested material, but in the evening (time interval 8) this was the case only in one of all 23 animals. These observations support the opinion that the smaller Exocoetus obtusirostris (6-17 mm) graze in the pleustal zone only during the day.

4.533 Night-positive neuston

1. According to HARTMANN (1970 b) there exist two possibilities as regards the feeding rhythm of larger Scomberesox saurus in the pleuston:

a) The behavior of Scomberesox saurus (55-113 mm) is in accordance with ZUSSER's rule (1956), that is, it grazes only during the times of dusk and dawn. The digestive rhythm would then be as follows: the food ingested during dusk would in the course of the digestive process pass the middle and distal portions of the alimentary tract, and would be evacuated by the latter part of day. On the other hand, food ingested during dawn would pass middle and distal parts of the intestine during the first half of night, and would be evacuated when the latter part of night begins. Such a feeding rhythm would necessarily lead to the conclusion that the pleustal domain does not serve at all as a grazing place for Scomberesox saurus (55-113 mm) since they enter the pleustal zone only after sunset and retire from there already before sunrise (cf. 4.32, p.45).

p. 36



Explanation of signs
■ = fresh intestinal contents
▩ = partly digested intestinal contents
small fishes = 6-50 mm; large fishes = 55-113 mm; ? = nature of intestinal contents obscure

Fig. 17. Vertical migration and feeding rhythm of Scomberesox saurus (6-113 mm).

b) The second possibility would be that — contrary to ZUSSER's categorical statement that planktotrophic pelagic fish do not feed by night — Scomberesox saurus (55-113 mm) feed only during dusk/dawn and during the night. Light conditions, which are especially favorable in the pleuston layer, seem to make such feeding habits feasible. In favor of this type of feeding rhythm is the fact that Scomberesox saurus (55-113 mm) did ingest large amounts of food in the net throughout the night, but this might be an irregular behavior elicited by the high plankton concentration in the net.

Although the time of food intake by Scomberesox saurus (55-113 mm) could not be narrowed down with certainty, a difference between the feeding rhythms of small and of large Scomberesox saurus became nevertheless visible. Small animals (6-50 mm) graze in the pleuston layer during daytime, whereas large individuals (55-113 mm) ingest food in lower levels during dusk and dawn, and perhaps also during the night in the pleuston. This difference in feeding habits between the length groups is illustrated in Fig. 17 (p. 87) which combines the results of vertical migration und feeding rhythms of this species.

Different from both length groups of Scomberesox saurus are the feeding rhythms of juvenile and adult Myctophydae which were caught in the pleustal layer exclusively during nights.

2. The most numerous species among the Myctophydae family is Gonichthys coccoi of which 524 individuals were obtained with the top net, middle net and lower net, and divided according to the following time intervals: first quarter of the night = time intervals 9-10, second quarter of the night = time intervals 11-12, third quarter of the night = 13-14, fourth quarter of the night = time intervals 15-16. In this manner, the number of Gonichthys coccoi in these individual time intervals were in 1967: 61-62-176-105; and in 1968: 0-74-19-27. The samples from the third and fourth quarter of the night were combined (46 exemplars). The vertical lines in Fig. 18 distinguish the results from 1967 by a solid line and those from 1968 by a broken line.

The condition of the stomach contents in the course of the night offered the following picture in regard to Gonichthys coccoi (Fig. 18, p. 91): The percentage of animals with fresh stomach contents were low both in

1967 and 1968 (20%, 33%) as compared to Scomberesox saurus measuring 55-113 mm in length (100%, 76%) (HARTMANN 1970 b). This proportion shifted slightly in the course of the night. Fresh food was found also toward the end of the night.

Partly digested food was, in 1967, constant and frequent at all time intervals (14-20%) while the percentage of animals whose intestines contained remains increased from the first quarter (10%) to the last quarter (34%) of the night. The percentage of animals with an empty stomach decreased slightly from 32% to 20% only during the last quarter of the p. 37
night. Using the 1967 material separate tests were performed for a) fresh, b) partly digested stomach contents, c) food remains, and d) empty stomach, to establish whether the hypothesis holds true that, between the four quarters of the night, the ratio 1:1:1:1 applies.

The hypothesis that the proportional values do not change significantly during the night was acceptable for cases a), b), and d).

How is this result to be interpreted? Against the presumption that Gonichthys coccoi eats only during nights, or exclusively during daytime, speaks the fact that the proportion of animals with fresh stomach contents stays constant throughout the night, and also that the diagrams do not exhibit any regularity. On the other hand, if Gonichthys coccoi would restrict its food intake to dawn and dusk, a percentage of more than 25% could be expected during the night of animals with fresh stomach contents; furthermore, for the diagrams which show the percentage of animals with stomach contents that are no longer fresh, obvious maxima could be expected. Under no circumstances does this species feed only during daytime in deeper layers, since the stomach contents of Gonichthys coccoi from the NW Atlantic (CRADDOCK 1969) consisted up to 50% of terrestrial insects (cf. p. 79).

This leaves only the conclusion that the Gonichthys population feeds by day and by night. This is supported by the fact that the percentage of stomachs with fresh, partly as well as extensively digested, or no food was about 25% each during all 4 time intervals of the night. Especially the low percentage of Gonichthys coccoi with fresh food in their stomach speaks for continuous food intake by the Gonichthys population. — It could also be quite conceivable that the myctophids, being the most massive among the ichthyoneuston, ingest additional food in the sub-pleustal layers of the trophically poor region sampled during the "Meteor" cruises. — However, the individual seems to pause between meals independently from the time of day, as judged by the percentage of Gonichthys coccoi found to have their stomach empty.

3. As a parallel investigation to that on Gonichthys coccoi, the five myctophid species Hygophum hygomi, Hygophum reinhardti, Myctophum nitidulum, Myctophum punctatum, and Symbolophorus veranyi, caught in 1967, were investigated as one unit. This material consisted of 128 animals which were caught during the four quarter-intervals of night-time in the following proportions: 24, 15, 64, 18 individuals (Fig. 18, p. 91). In comparison with the diagrams that relate to Gonichthys coccoi, the most striking feature of Fig. 18 is the low percentage of animals with empty stomachs (0-14%). This causes an elevation of the percentages for the other three diagram series that comprise the extent of digestive states in the digestive tract (fresh food, partly digested, food remains). Similar to Gonichthys coccoi, those diagrams that illustrate the percentage of animals with freshly ingested food, or with empty stomachs, do not show any regularity. In total, the limited and heterogenic material is not indicative of differences between the feeding rhythm of the five myctophid species and Gonichthys coccoi.

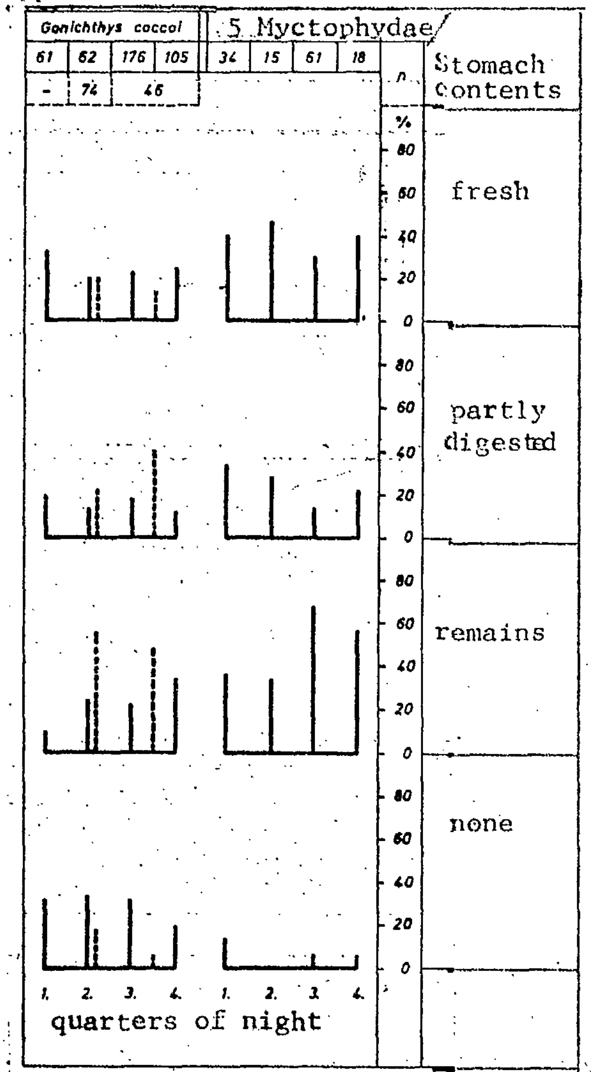


Fig. 18. Condition of stomach contents in various species of Myctophydae. — solid lines = 1967 broken lines = 1968

In the same manner as for Gonichthys coccoi, the hypothesis that the various digestive stages of the stomach contents (fresh, partly digested, remains, and empty stomach) remain constant in their proportions throughout the night, was tested also for the 5 myctophid species.

Separately for each digestive stage it was checked wether the proportion of these stages remained 1:1:1:1 throughout the 4 quarters of the night. The result of the chi-square test showed that the percentage of animals with fresh stomach contents and those with empty stomachs is not subject to statistically significant changes.

p. 38

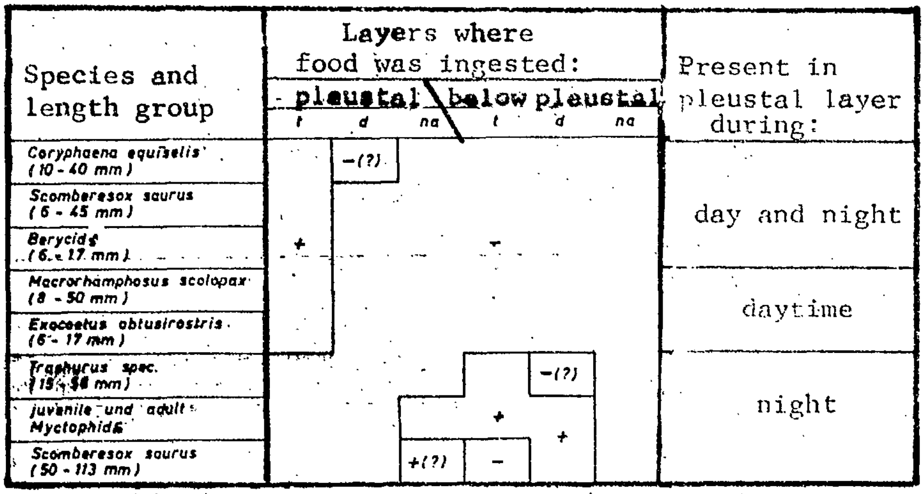


Fig. 19. Time and location of food intake.
+ = feeding activity
− = no feeding activity
? = uncertain
t = during daytime
d = " dusk or dawn
na = " the night

It can therefore be assumed that, similar to Gonichthys coccoi, these five Myctophidae maintain food intake during both day and night.

4. The last species whose feeding rhythm shall be discussed is Trachurus spec. (15-56 mm); 50 animals from 9 top-net and 3 lower-net samples from the Great Meteor Seamount region (spring 1967) were examined: Unmistakably fresh food was found in 4 of 11 Trachurus spec. from the first portion of the night, whereas empty stomachs were found in 2 of 11 animals during the first half of night, and 35 out of 39 specimens during the latter half. As judged by these data, Trachurus spec. (15-56 mm) does not graze in the pleustal domain.

Fig. 19 summarizes the results obtained so far on time and location of food-intake by ichthyoneuston. This illustration shows once again that the day-positive and the pleuston-constant fishes are similar in their feeding habits: They ingest only during daytime and exclusively in the pleustal domain. By contrast, the behavior of night-positive animals seems to differ: Most night-positive species ingest their food during their ascending or descending vertical movements during dusk or dawn, and probably do not interrupt food intake during the night either, while they are staying in the pleustal layer (juvenile and adult Myctophidae, large Scomberesox saurus (50-113 mm).

During daytime in deeper layers, the behavior of night-positive species seems to differ from one another: The large Scomberesox saurus(50-113 mm) do not ingest food then, whereas the Myctophydae probably feed also during daytime in deeper layers. Trachurus spec. (15-56 mm), on the other hand, does probably feed only during daytime and exclusively in subpleustal layers. Therefore, this species uses the pleustal domain not for trophical purposes but merely as a niche to be visited at regular intervals.

The question whether the pleuston serves as a pasture for ichthyoneuston, can therefore not be answered generally. It applies without limitation for those fishes among our material that live constantly or exclusively during daytime in the pleustal layer. Also the Myctophidae feed during the night at the surface. For the larger Scomberesox saurus, pleustal food intake was not established with certainty, and for one species (Trachurus spec.), it can be assumed that food is not ingested in the pleustal layer.

4.54 Competition for food

4.541 Percentage of individual food types

Fig. 20 is a compilation of the results described in chapter 4.5 so far. According to this, the contents of the digestive tracts consist of three types which correspond to the following three groups of ichthyoneuston:

1) smaller fishes that feed on neuston during daytime,

2) larger fishes that feed on neuston during daytime,

3) fishes that do not ingest neuston during daytime.

The smaller fishes that feed on neuston during the day consisted of 5 individual groups: small Exocoetus (6-15 mm), larger Exocoetus 16-33 mm), very small Scomberesox saurus (16-30 mm), and small Macrorhamphosus scolopax (8-22 mm). The group of larger fishes that feed on neuston by day is made up by certain length groups of 4 species: larger Macrorhamphosus scolopax (23-50 mm), medium Scomberesox saurus (31-45 mm), Coryphaena equiselis (10-40 mm), and the berycid (6-17 mm). Because of its body size, the berycid does actually belong to the preceding major group, but the capacity of its mouth obviously permits the berycid to ingest relatively voluminous pieces. The following fishes were combined to the group that does not feed on neuston by day: Trachurus spec. (15-56 mm), five Myctophydae as a subgroup, Gonichthys coccoi, and the larger Scomberesox saurus (46-113 mm). The five myctophid species that made up the subgroup were: Hygophum hygomi, Hygophum reinhardti, Myctophum nitidulum, Myc- p.3
tophum punctatum, and Symbolophorus veranyi.

The results shown in Fig.20 (p.95) are based on material of varying extent. Identifiable intestinal contents were available in the following: 48 smaller Exocoetus (6-15 mm; 45 Exocoetus obtusirostris and 3 Exocoetus volitans), 29 larger Exocoetus (16-33 mm; 25 Exocoetus obtusirostris and 4 Exocoetus volitans), 204 very small Scomberesox saurus (6-15 mm), 162 small Scomberesox saurus (16-30 mm), 110 medium Scomberesox saurus (31-45 mm), 207 large Scomberesox saurus (46-113 mm), 20 smaller Macrorhamphosus scolopax (8-22 mm), 36 larger Macrorhamphosus scolopax (23-50 mm), 14 Coryphaena equiselis, 7 berycids, 15 Trachurus spec., 108 specimen of the family of Myctophidae, and 262 Gonichthys coccoi. The evaluation of the berycids led despite the low number of 7 animals to results which harmonize with those obtained from the other species that feed on neuston during the day.

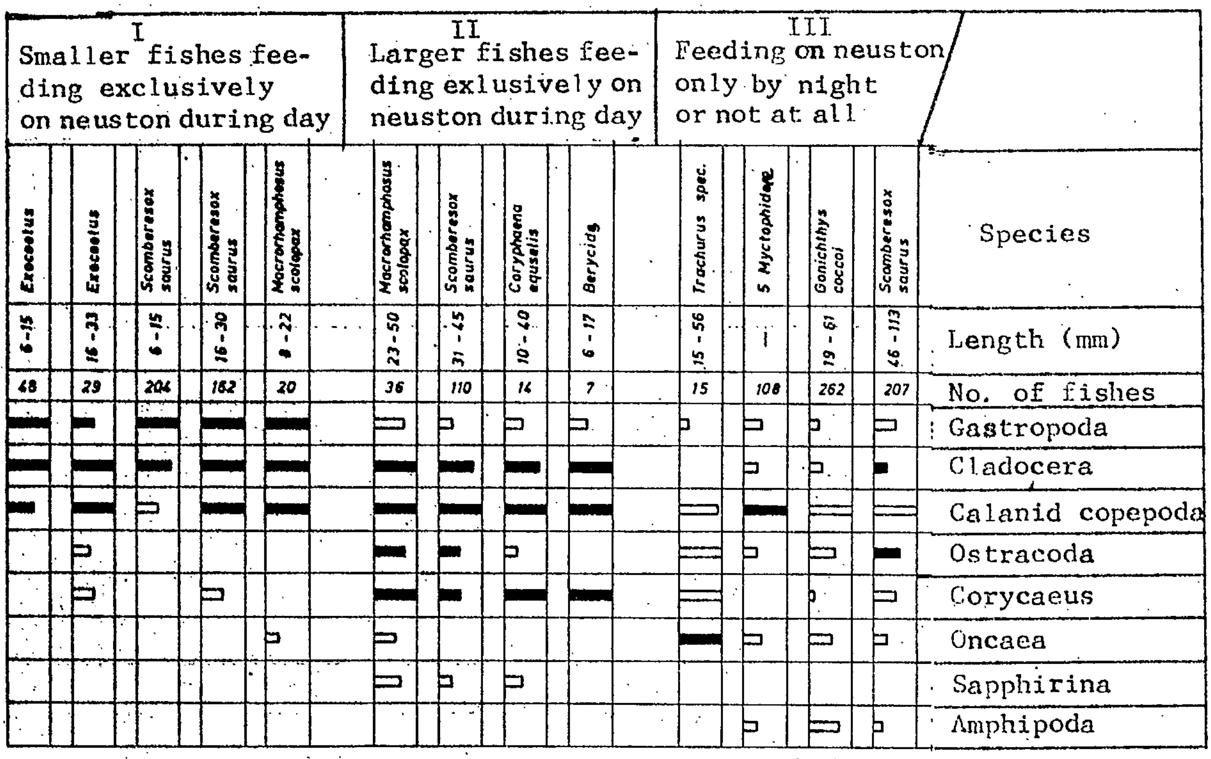


Fig. 20. Simplified graphic illustration of intestinal contents in various ichthyoneuston species. As described before (Fig. 12, p. 66; text pp. 62-63), black columns indicate that more than 49% of the fishes contained more than two specimens of the particular type of food in their digestive tract. Full-length column = >39%; 1/40 of complete column = 1%.

A high percentage of gastropoda was characteristic for the smaller fishes that fed on neuston during daytime. The smaller Exocoetus (6-15 mm), small Scomberesox saurus (6-15 mm, 16-30 mm), and small Macrorhamphosus scolopax (8-22 mm) had each consumed more than 40% gastropoda, mostly in larger amounts (black column). Only among larger Exocoetus (16-33 mm) there were less than 40%, namely 20% that had gastropoda in their stomach. Next to gastropoda, the cladocera were characteristic among intestinal contents of the smaller fishes that were feeding during daytime. Cladocera were found, in most cases in larger amounts, in more than 40% of Exocoetus (6-15 mm, 16-33 mm), of small Scomberesox saurus (16-30 mm), and of small Macrorhamphosus scolopax (8-22 mm). However, of the smallest Scomberesox saurus (6-15 mm) only 30% were found with cladocera. The calanid copepoda also played an important part already in small fishes ingesting neuston during the day. More than 40% of the larger Exocoetus (16-33 mm), of the small Scomberesox saurus (16-30 mm), and the small Macrorhamphosus scolopax (8-22 mm) had ingested calanid copepoda. For the youngest stages among the fishes that fed on neuston during the day, the calanid copepoda had not yet reached the importance observed in later stages. Only 26% of the small Exocoetus (6-15 mm) and 20% of the small Scomberesox saurus (6-15 mm) had consumed calanid copepoda. Finally, the importance of Coryaceus gained grounds for the largest among the smaller fishes feeding on neuston during daytime. The copopod Corycaeus was found in 22% of the larger Exocoetus (16-33 mm), and in 20% of the Scomberesox saurus measuring 16-30 mm.

The difference between the larger fishes that fed on neuston during p. 4 the day and the smaller ones was found to lie in the decreased percentage of gastropoda among the food of the larger group. The percentage of gastropoda-positive fishes among the larger Macrorhamphosus scolopax (23-50 mm) was 32%, among medium-sized Scomberesox saurus (31-45 mm) it was 12%, and 16% for both, Coryphaena equiselis and the berycid. In these cases, the gastropoda had mostly been ingested in the form of single specimens.

In contrast to the smaller fishes that fed on neuston during the day, large amounts of Corycaeus were found in the larger fishes whose food-intake took place by day in the pleustal layer, namely in more than 40% of the larger Macrorhamphosus scolopax (23-50 mm), of Coryphaena equiselis and the berycid, as well as in 22% of the medium-sized Scomberesox saurus (31-45 mm). Ostracoda, whose presence in smaller fishes was an exception (in 16% of Exocoetus measuring 16-33 mm, in form of single specimens), occurred usually in large amounts (black columns) in the larger group of fishes that feed on neuston during the day. They were found in 32% of the larger Macrorhamphosus scolopax (23-50 mm), in 22% of medium-sized Scomberesox saurus (31-45 mm), and single exemplars were present in 10% of Coryphaena equiselis. Especially characteristic for the stomach contents of larger fishes among those feeding on neuston during the day was Sapphirina: Mostly in the form of single individuals in 24% of the larger Macrorhamphosus scolopax (23-50 mm), in 10% of medium-sized Scomberesox saurus (31-45 mm), and in 16% of Coryphaena equiselis. In both the other main groups, namely the small fishes that fed on neuston during daytime, and fishes that did not consume any neuston during the day, Sapphirina was not observed. Calanid copepoda were found still more frequently (more than 40%) than in the smaller fish that consumed neuston during the day. Cladocera had also been ingested regularly and in great numbers: More than 40% of the larger Macrorhamphosus scolopax (23-50 mm) and the berycid, as well as 32% of the medium-sized Scomberesox saurus (31-45 mm) and Coryphaena equiselis had consumed cladocera.

The group of fishes that do not feed during the day on neuston is, in contrast to both previously discussed main groups, composed of larger animals. As can be seen from Fig. 20 (p.95), the fishes that do not feed on neuston during daytime are characterized by the fact that none of the food types was especially prominent (short, white columns are domineering). The percentage of gastropoda is reminiscent of the group of larger fishes that do feed on neuston during the day. Here also, 8-20% of the animals had ingested gastropoda mostly in the form of single specimens. The percentage of ostracoda as part of the stomach contents is also very much alike in both these groups: Trachurus spec. more than 40%, the 5 Myctophydae 14%, Gonichthys coccoi and large Scomberesox saurus (46-113 mm) 26%. In contrast to the group that did feed on neuston during the day, cladocera were only seldom found in fishes that do not graze on neuston during daytime: The five myctophid species, Gonichthys coccoi, and large Scomberesox saurus (46-113 mm) each contained 10%. While calanid copepoda were still ingested by many of these animals, they were found only in the form of single specimens in 36% of Trachurus spec., and in more than 40% of the remaining species in this group. The copepod Corycaeus was also found only in single instances in animals that do not feed on neuston during the day, which is in contrast to the findings in the group of larger fish that do. The amount of Corycaeus-positive fishes varied between 0% and more than 40%. Characteristic for the intestinal contents of fishes that do not feed on neuston during the day was Oncoea, found in 10% to more than 40% of these animals. This species was otherwise found only in Macrorhamphosus scolopax (8-50 mm) whose food-intake is during daytime. On the other hand, amphipoda were detected only in those fishes that do not feed in the pleustal domain during the day (0-24%).

The great variety of trophic organisms found regularly, but seldom in large amounts, which distinguishes this group from that feeding on neuston during the day, indicates that a wider choice of food is offered to fishes that do not graze in the pleustal domain during daytime (perhaps also on account of the capacity of their jaws).

As the most important result shown in Fig. 20 (p.95), the homogeneity the intestinal contents within each of the three main groups deserves special mention. This uniformity indirectly confirms the results obtained from individual groups, and speaks in favor of the participation of identical sensory organs in the hunt for food. Furthermore, the homogeneity of intestinal contents is indicative of a strong competition for food within each of the three main groups. The specialists among our ichthyoneuston species are exceptions (cf. 4.522, p.79).

With the purpose of expressing the degree of competition for food between two groups of fish in the form of numerical values, comparisons were made between the lengths of columns that indicated homologous food types for both fish groups. The extent to which the paired columns were overlapping was taken as the degree of competition for this type of food. For the comparison of two fish species, the columns of all food types were paired in this manner and the extent to which the individual pairs were overlapping was noted. The total of these congruential stretches furnished for each pair of comparable fish groups a numerical value which was all the higher, the longer the congruency of the paired columns. The difference between black and white columns was also taken into consideration in that the extent to which a black and a white column overlapped was dimidiated in subsequent calculations. 1/20 of column length was considered as gauge point 1.

Table 9. Competition among ichthyoneuston for the various types of food. p. 41

	I				II				III			
	Exocoetus (16—33)	*Scomberesox saurus* (6—15)	*Scomberesox saurus* (16—30)	*Macrorhamphosus s.* (8—22)	*Macrorhamphosus s.* (23—50)	*Scomberesox saurus* (31—45)	*Coryphaena equis.*	Berycid.	*Trachurus* spec.	5 Myctophids	*Gonichthys coccoi*	*Scomberesox saurus* (46—113)
I *Exocoetus* (6—15)	43	40	63	53	50	23	33	36	8	19	11	13
Exocoetus (16—33)		30	60	50	54	48	50	52	29	32	25	34
Scomberesox saurus (6—15)			40	40	27	22	24	23	12	11	20	20
Scomberesox saurus (16—30)	$\tilde{x} = 48$			60	52	42	46	49	21	26	17	29
Macrorhamphosus scolopax (8—22)					52	37	40	44	14	31	20	25
II *Macrorhamphosus scolopax* (23—50)						67	74	68	36	43	34	42
Scomberesox saurus (31—45)	$\tilde{x} = 41$						58	50	25	30	24	34
Coryphaena equiselis					$\tilde{x} = 64$			65	29	36	24	30
Berycid.									24	29	18	27
III *Trachurus* spec.										25	42	41
5 Myctophids	$\tilde{x} = 21$				$\tilde{x} = 30$						43	33
Gonichthys coccoi									$\tilde{x} = 38$			45

I = small fish feeding on neuston by day
II = larger fish feeding on neuston by day
III = the rest, not feeding on neuston by day
More explanations in the text.

The values for the competition among fish groups for their food, calculated in this manner, are shown in Table 9. The Table furnishes first of all 78 values indicating the competition of individual groups. From these individual values, 6 medians were calculated which characterize the average of competition for food within each of the three main groups, as well as of the three main groups with one another.

from p. 40

p. 41 cont'

Table 9 illustrates the following results: The strongest competition for food exists within the group of larger fishes that feed on neuston during the day (highest individual value: 74, $\tilde{x} = 64$). A considerable degree of competition for food can be observed also among the small fishes that feed during daytime on neuston ($\tilde{x} = 48$), whereas the

Table 10. Competition for food among ichthyoneuston in regard to the size of atlantide shells.

I = small fish feeding on neuston by day
II = larger fish feeding on neuston by day
III = fishes not feeding on neuston by day
Detailed explanation for Table 10 in text (p. 111)

	I: *Scomberesox saurus* 6—15 mm	I: *Scomberesox saurus* 16—30 mm	I: *Macrorhamphosus scolopax* 8—22 mm	II: *Macrorhamphosus scolopax* 23—50 mm	II: *Scomberesox saurus* 31—45 mm	III: *Gonichthys coccoi* 20—61 mm	III: *Scomberesox saurus* 46—113 mm
I *Scomberesox saurus* 6—15 mm		59	67	18	40	0	15
Scomberesox saurus 16—30 mm			44	44	67	11	28
Macrorhamphosus scolopax 8—22 mm	$\bar{x} = 57$			11	29	0	17
II *Macrorhamphosus scolopax* 23—50 mm	$\bar{x} = 35$				77	29	40
Scomberesox saurus 31—45 mm						29	45
III *Gonichthys coccoi* 20—61 mm	$\bar{x} = 12$			$\bar{x} = 36$			83

heterogenic group of fishes not feeding on neuston by day exhibits a lower degree of [redacted] competition for food ($\bar{x} = 38$). The competition for food among both the main groups that feed on neuston by day reaches a high value ($\bar{x} = 41$) which is even greater than the competition for food within the group that does not feed on neuston by day ($\bar{x} = 38$). Between the larger p. 42 fish that feed on neuston by day and fishes that do not feed on neuston by day, the competition for food becomes, then, considerably weaker ($\bar{x} = 30$), and the lowest value is reached in the competition for food between small fishes feeding on neuston by day and fishes that do not feed on neuston during daytime, two groups which show also extreme differences in their lengths ($\bar{x} = 21$, lowest value 8).

So far, upon evaluation of Table 20, interest was focused on the group of grazers, and the question was what type of prey the individual fish group had ingested. In the following, the importance of the individual groups among trophic animals will be discussed.

Mollusks were considered by LEBOUR (1933) as the principal food of the plankton grazers, especially of their younger stages, and ZAITSEV (1961) considered the mollusks as the principal food of the young stages of ichthyoneuston in the Black Sea. Fig. 20 (p.95) shows on the basis of our material that gastropoda were of importance only to the small fishes that fed on neuston during the day, but played only a minor role for larger fishes. This observation indicates that our material contained length groups which the drifting device of ZAITSEV (Table 1, p.11) was unable to catch.

Cladocera were an important food for fishes feeding on neuston by day. On the other hand, only few of the fishes that did not feed on neuston by day had ingested cladocera.

Copepoda have been named unanimously by LEBOUR (1917), MIELCK (1925), COVILL (1959), and MARAK (1960) as an important food for young stages. Special importance seems to be attached to the copepoda in the boreal domain. In addition to corresponding statements in the literature, this opinion is supported also by the findings in stomach contents of 340 *Onos cimbrius* (6-43 mm total length), and *Onos mustelus* (8-39 mm total length) from the pleustal layer of the North Sea: 65-100% of the fishes from the individual 3 mm length groups had ingested some copepoda.

The heterogenic group of calanid copepoda, which makes up the largest part of all copepoda, played an important role also in the subtropical pleustal domain. Especially in the stomachs of fishes that feed by day have they been found in large amounts in more than 40% of the animals.

However, as a rule, night-positive ichthyoneuston had ingested calanid copepoda only in the form of single specimens (white columns), which is explained by the greater variety available in deeper strata, as well as by night at the surface, and by "scattering in the darkness" (CUSHING 1951).

Ostracoda were part of the ingested food only in ichthyoneuston of advanced length: They were present in the larger fishes feeding by day (0%-22%), and also in those not feeding on neuston by day (14%-40%).

Multiple Corycaeus among intestinal contents were characteristic for larger fishes feeding in the pleustal layer by day.

The related copepod Oncaea had been ingested by all fishes that do not feed in the pleustal domain by day, but also by Macrorhamphosus scolopax (8-50 mm) who does feed on neuston during daytime. The irregular distribution pattern of Oncaea (Fig. 20, p.95) may perhaps be connected with the fact that this copepod was found only during spring among the intestinal contents of fishes from the Great Meteor Seamount, the primary sampling region. Oncaea was also almost completely missing from the corresponding plankton samples (WEIKERT, oral communication).

Sapphirina — insignificant in its number — occurred only in larger fishes that feed during the day in the pleustal layer.

As for amphipoda, it was stated by LEBOUR (1919-1922, p.267) that they are seldom ingested by young stages, but frequently by adult fishes. Analogous to LEBOUR's result, amphipoda were found almost exclusively in the alimentary tract of night-positive ichthyoneuston. This may be due to the relative size of amphipoda and their diurnal migration.

The results on the intestinal contents of ichthyoneuston shall here again be compared in their entirety with LEBOUR's observations (1917-

1933) from the boreal pelagic domain: Tintinnids, invertebrate eggs, cladocera, copepoda, amphipoda and mollusks played a similar role as food for young stages in LEBOUR's material as here for the subtropical ichthyoneuston. However, in the subtropical pleustal domain, not many species were found to practice specialization in the choice of their food; surprising was furthermore the homogeneity of intestinal contents in fishes from equal length groups whose presence in the surface layer coincided. This deviation from LEBOUR's findings can be explained with a different plankton composition in both these climatic regions: In adaptation to the food shortage (cf. 4.7, p.121) and the great variety of species in the subtropical pleustal domain, the fish population will here ingest generally any piece of suitably-sized food. However, it was observed also in the boreal region by MARAK (1960), who collected with a ring-shaped trawl, from the surface, larval and postlarval Gadidae consisting of three species, and by COVILL (1959) on the basis of larval and postlarval Ammodytes, that the fish ingested what was found most frequently, and that they were selective only in regard to the size of their food.

The following compilation summarizes the food types that were most characteristic for ichthyoneuston:

1. For all fishes feeding in the pleustal layer by day: great amounts of cladocera, and of calanid copepoda;
2. for small fishes feeding in the pleustal layer by day: great amounts of mollusks;
3. for large fishes feeding in the pleustal layer by day: great amounts of Corycaeus, isolated Sapphirina (both cyclopoid copepoda); p.43

4. for fishes not feeding in the pleustal layer by day: amphipoda;

5. for larger ichthyoneuston: ostracoda.

Following the discussion on plankton organisms that serve as food for ichthyoneuston, it shall now be outlined for which species the fishes of the pleustal domain could serve as food: As the higher links of the trophical chain should be considered, besides birds (ZAITSEV 1968), the fishes Mola, Manta (NORMAN & FRASER 1963), Coryphaena (GIBBS 1959, KOJIMA 1961) and tuna (SUND & RICHARDS 1965). ZAITSEV (1961) found neuston in the stomachs of skipjacks, Scombridae, and pelamyds [young tuna], among others. Smaller fishes were preyed on also by coelenterata (e.g., photograph in FRASER 1962). A Macrorhamphosus scolopax who successfully avoided the tentacles of Physalia for a full day in an aquarium, fell then victim along with other fishes to a pleustonic brachyura. Isopoda (Idotea metallica, identif. WEIKERT) were observed to skeletonize their prey even while being already in the concentrator (compare HERRING 1969). Important are perhaps also the cephalopoda. BAKER (1960) repeatedly observed in the NE Atlantic by night Ommastrephes pteropus that had come to the surface and fed on small Scomberesox and Myctophydae. However, these cuttlefish may have been lured by the ship's artificial illumination to the immediate surface to which they are obviously not limited, since they were spotted at the same time, with the help of a camera and depth cable, in depths of up to 1,000 m.

4.542 Size of trophic animals

4.5421 Introduction

While, in chapter 4.541, merely the number and types of animals were discussed that were found as food in the digestive tracts of ichthyoneuston, we shall discuss under this heading the size of food objects. Comparison of the length ranges of the ingested organisms will shed additional light on the competition among individual fish groups for the available food.

MARAK (1960) observed (cf. 4.541, p.104) in larvae and juveniles that the difference between stomach contents was not so much in the type of food, but rather the size of food objects, and that with increasing size of the fish the average size of food objects increased as well. — The lower limit of object size is, according to YASUDA (1957), dependent upon the "mesh size" of the gills (YASUDA investigated five oceanopelagic fish species of appr. 20-50 mm in length). The maximal volume of ingested food objects is likely determined mainly by the capacity of the fish's mouth, but G.F. HARTMANN (1958) demonstrated that structure and reaction of the prey also play a role here.

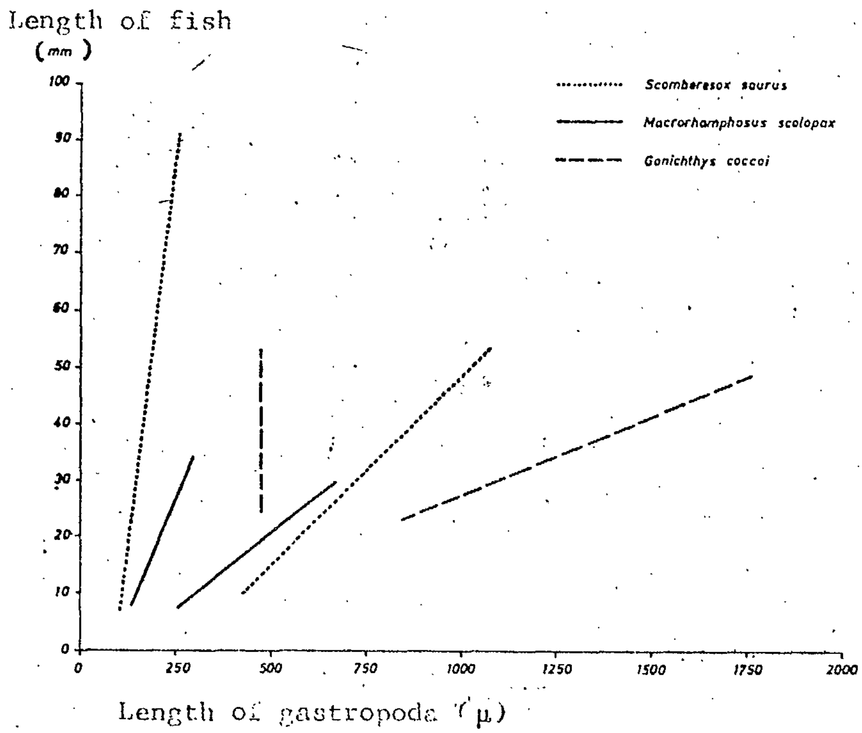


Fig. 21. Maximal and minimal lengths of atlantid shells consumed by three species.

In the present work, the size of food objects found in the digestive tracts was determined on hand of the following material:

Scomberesox saurus	(6-113 mm):	683 animals,
Gonichthys coccoi	(20- 61 mm):	262 animals,
Macrorhamphosus scolopax	(8- 50 mm):	56 animals.

Calculations for the length of food objects were limited to one plank- p. 44
ton group, the atlantids (incl. all gastropoda with similarly shaped shells). The sizes of gastropoda shells -- considered here as indicator of the size limits still acceptable to the fish -- represent of course merely an approximate norm. Other food objects may vary within different size ranges depending upon their form and reaction. Atlantids are especially suited for length determinations because size and shape of their shells do not change in the digestive tract nor upon fixation, and furthermore, because they are consumed frequently and by many length groups of neuston fish. The maximal diameter of the mollusk shells was measured individually with the help of an ocular micrometer (to 1/40 of a millimeter = 1 graduation mark). In-between values were rounded off to the closest graduation mark. Fish-lengths were measured to the exact mm, always taking the full millimeter as the group median. For each one-millimeter group of fishes, the maximum and minimum lengths of gastropoda shells from their digestive tracts were determined; the points from the periphery of the field were then plotted against the length of fishes, separately for each fish species, in the form of three graphs. Out of 683 Scomberesox saurus, 22 animals furnished extreme values, of the 56 Macrorhamphosus scolopax there were 30, and of the 262 Gonichthys coccoi there were 27 animals with extreme values. In each of the three graphs, the peripheral points of the field thus plotted [redacted] were connected so that this line became represen-

tative of the length range of gastropoda shells consumed by the individual fish species. All three graphs within the field of points (HARTMANN 1969a) are combined in Fig. 21 (p. 106) in a simplified manner.

4.5422 Results

1. Scomberesox saurus. The minimum lengths of gastropoda shells showed only minor variations between individual fish groups. They were at 95 μ for the smallest Scomberesox saurus (6-15 mm), and at 310 μ for the largest among the Scomberesox saurus (92 mm) sampled. Starting at 15 mm fish length, the length of the smallest gastropoda shells increased at first rapidly, then more slowly. A break in the minimum curve at the 15 mm point of fish length might indicate that, from this length on, it is no longer worth bothering for Scomberesox saurus to ingest the smallest gastropoda.

The maximal lengths of consumed gastropoda shells increased sharply with advancing fish length. While fishes measuring 6 mm had consumed gastropoda shells of up to 200 μ, the Scomberesox saurus measuring 54 mm had in their digestive tract gastropoda of 1070 μ. A break in the maximal curve at the 8 mm point of fish length might indicate that the smallest Scomberesox saurus still lack the technique to obtain those gastropoda sizes that would correspond to the capacity of their jaws.

Particularly worth mentioning seems the divergence of the minimum and maximum values with increasing length of the fish groups. This indicates that the fishes gave up consuming the smallest gastropoda at a much slower rate than that at which their ability of catching the larger gastropoda was increasing. Thus, the fishes continued to make use, as long as possible, of the richer populated lower gastropoda classes.

2. Gonichthys coccoi. The length range of Gonichthys coccoi shifted, in comparison to Scomberesox saurus, upwards while that of the gastropoda shells moved to the right. The stomach contents of the smallest Gonichthys coccoi (23 mm) showed gastropoda shells starting at 475 μ, while those in the largest Gonichthys coccoi (54 mm) started with 500 μ. In contrast to Scombersox saurus, the minimum length of consumed gastropoda shells remained almost constant in Gonichthys coccoi. It is possible that light conditions by night, which make recognition of smaller gastropoda difficult, may represent a limiting factor for Gonichthys coccoi.

The maximal lengths of consumed gastropoda varied in Gonichthys coccoi between 840 μ at 23 mm fish length, and 1750 μ in fishes measuring 46 mm. Therefore, similar to findings in Scomberesox saurus, the difference between maximum and minimum lengths of ingested gastropoda shells increased here also with progressing length of the fish.

3. Macrorhamphosus scolopax. The position of this graph shows a similar tendency to those of both previous species. The length range of the gastropoda lies within the limits of that established for Scomberesox saurus. Also in the case of Macrorhamphosus scolopax, an increased broadening of the length range of consumed gastropoda shells can be observed with increasing length of the fish groups. Very instructive was the examination of the stomach contents from one Macrorhamphosus scolopax (49 mm long) who had stayed for about a week in the ship's aquarium. Stomach as well as intestine contained exclusively gastropoda shells. Apparently, these gastropoda were the only morsels of food that succeeded in passing the filter system and landing in the basin with the fish. They were, with 150 μ, considerably smaller than would have to be expected according to

the graph (375 μ) in Fig. 21 (p.106). This observation indicates that a hungry fish accepts a broader length range of individual pieces for his food (lowering of stimulus threshold).

Based on Fig. 21, the competition for food as related to the size of the atlantid shells was calculated for 21 pairs of fishes (see below). In order to obtain comparative values to Table 9, which derived the degree of competition for food among fishes from the proportions of 8 principal food groups in their stomachs, the same length groups and the same three p. 45
main groups as in Table 9 were utilized for this purpose:

I. Smaller fish feeding on neuston by day
<u>Scomberesox saurus</u> 6-15 mm
<u>Scomberesox saurus</u> 16-30 mm
<u>Macrorhamphosus scolopax</u> 8-22 mm

II. Larger fish feeding on neuston by day
<u>Scomberesox saurus</u> 31-45 mm
<u>Macrorhamphosus scolopax</u> 23-50 mm

III. Other fish, not feeding on neuston by day
<u>Scomberesox saurus</u> 46-113 mm
<u>Gonichthys coccoi</u> 20-61 mm

The numerical values indicative of the degree of competition for food among individual fish groups were calculated on the basis of group medians (e.g., in the case of <u>Scomberesox saurus</u> 6-15 mm on the basis of the mean fish length of 10.5 mm) according to the following formula:

$$N = 100 \frac{J - a}{A - i}$$

N = Competition for food as related to size of atlantid shells;
A = the greater of the two maximal lengths of gastropoda shells to be compared (Fig. 21, p. 106 — unit of measure: 10 μ = 1);
i = the smaller of the two minimum lengths of gastropoda shells to be compared (Fig. 21, p. 106 — unit of measure: 10 μ = 1);
a = the smaller of the two maximal lengths of gastropoda shells to be compared (Fig. 21 — unit of measure: 10 μ = 1);
J = the greater of the two minimum lengths of gastropoda shells to be compared (Fig. 21 — unit of measure: 10 μ = 1).

The values calculated in this manner are shown in Table 10 (p.101).

On account of the factor 100, contained in the formula, the values in Table 10 appear in the same order as in Table 9, and are to be read in the same manner: Large numbers represent in both Tables a high degree of competition for food.

Table 10, which is designed in the same fashion as Table 9 except that it covers only 21 pairs instead of the 78 pairs of fish groups in Table 9, illustrates the following results: A strong competition in regard to the size of the atlantid shells exists between pairs of each of the three main groups (I = 44-67; II = 77; III = 83). Within both of the two groups feeding by day (I and II), maximal values were seen also in Table 9 (I = 48; II = 64). However, for <u>Scomberesox saurus</u> (46-113 mm) and <u>Gonichthys coccoi</u> (20-61 mm), which represent in Table 10 the only pair of group III, Table 10 shows a high degree with $\bar{\bar{x}}$ = 83, while only a medium degree of competition for food is shown in Table 9 with $\bar{\bar{x}}$ = 45.

Table 9 and 10 again correspond in regard to the competition for food between both of the main groups that feed in the pleustal domain by day: Table 9 with $\bar{\bar{x}}$ = 41 and Table 10 with $\bar{\bar{x}}$ = 35 point to a moderate degree of competition for food. An additional parallel in both Tables exists with regard to the competition between the two main groups II and III. According to Table 10 ($\bar{\bar{x}}$ = 36) and Table 9 ($\bar{\bar{x}}$ = 30), these two groups compete only moderately . Finally, both Tables agree with respect to the competition for food between the small day-feeder and those fishes that do not feed in the pleustal layer by day (groups I and III). Both Tables indicate an extremely low degree of competition for food (Table 9: $\bar{\bar{x}}$ = 21, Table 10: $\bar{\bar{x}}$ = 12).

The figures in Table 9 correlate positive with the 21 values in Table 10 in that r = 0.70 (95% confid. $0.[illegible]2 \leqq \varrho \leqq 0.85$). This value shows once again: Those groups whose intestinal contents showed certain similarities as to amount and type of food, were usually also great rivals with regard to the size of their food, whereas groups who competed little for type and amount of food had generally consumed food specimens (atlantids) of different sizes. Therefore, among the species investigated, there existed a similar degree of competition for type and size of the available food.

Chapter 4.7 (p. 121) discusses the results from the examinations of intestinal contents on the basis of broader implications.

4.6 Regional and seasonal differences between populations of the areas sampled

4.61 Regional distribution within areas sampled

In the area sampled in 1967, 10 groups of fish can be distinguished according to their regional distribution.

From their distribution results a total of five regions (Fig. 22, p. 113) which are distinct also in their position to the mainland, their plankton content, and the surface temperature of the water (Fig. 22):

1) two upwelling regions in coastal waters (Stations 56-58, 67-68);
2) the coastal region (Stations 44-55, 59-66, 69);
3) the region between Cape St. Vincent and Madeira (Stations 70-107);
4) the region between Madeira and the Great Meteor Seamount (Stations 108-124);
5) region of the Great Meteor Seamount (Stations 8-43, V-1—V-32, 125-175).

p. 46

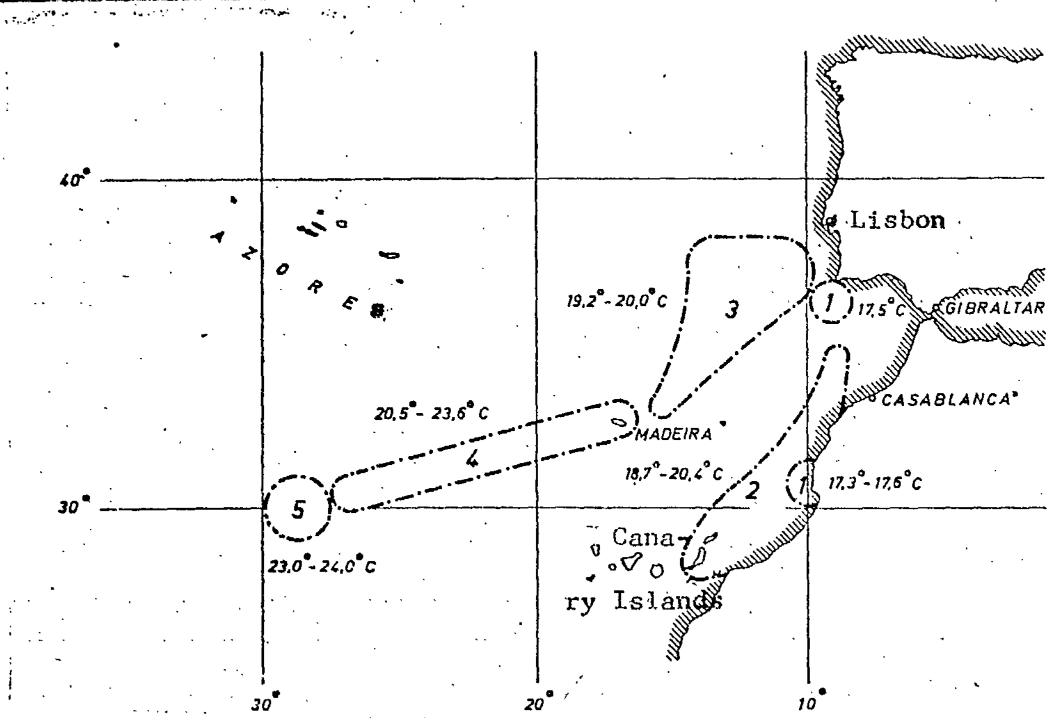


Fig. 22. Regional distribution 1967. Encircled numbers = number of region (see text).
Regional surface temperatures of water are indicated as °C.

In the following list, the abreviation "Sp" means that the particular species was found in the Great Meteor Seamount regions during spring only, whereas "Su" indicates that the species mentioned was there caught during the summer months only. The numbers proceeding the information refer to the number of regions shown in Fig.22 (see also previous page). from p. 45

Regional findings: p. 46 cont'

(1-5) throughout entire region incl. upwelling areas
Myctophum punctatum (Su)
Scomberesox saurus

(2-5) throughout entire region except upwelling areas
Gonichthys coccoi
Myctophid larvae
Macrorhamphosus scolopax (Sp) (in coastal region only in 1968)

(1) in upwelling waters only
Belone belone

(2) in coastal region only, except upwelling areas
Species C
Exocoetidae D II b

(3) strictly oceanic, East of Madeira
Species D

(2-3) East of Madeira, except upwelling areas
Species B
Symbolophorus veranyi
Onos spec.

(3-5) in the entire oceanic region
Hygophum reinhardti

(4-5) West of Madeira only
Exocoetus obtusirostris (Su)
Exocoetus volitans (Su)
Danichthys rondeletii (Sp)
Exocoetidae C 9 (Su)
Coryphaena hippurus (Su)
Coryphaena equiselis (Su)
Centrobranchus nigroocellatus
Myctophum nitidulum

(5) in Great Meteor Seamount region only
one berycid
Trachurus spec.
Nealotus tripes (Su)

(Sp 5/ in Great Meteor Seamount region during spring,
Su 1-3) East of Madeira during summer
Hygophum hygomi

This distribution is determined, among others, by three factors. First of all, water depth plays an important part; for example, *Belone belone* (region # 1) attaches its eggs to plants, and species C (region # 2) has barbels, therefore the adult life is spent at the bottom. Fig. 23 (p.115) shows that the neustonic stages of *Belone belone* were caught predominantly at or close to the shelf. By contrast, the myctophids of the pleuston preferred, according to Fig. 24 (p.116), particularly the oceanic waters off the edge of the shelf; In 1968, in the pleustal region above the shelf, not one myctophid was caught. This distribution of the Myctophidae is due to the fact that, by day, they are staying at a depth of 200-500 m (BECKER 1967).

p. 47

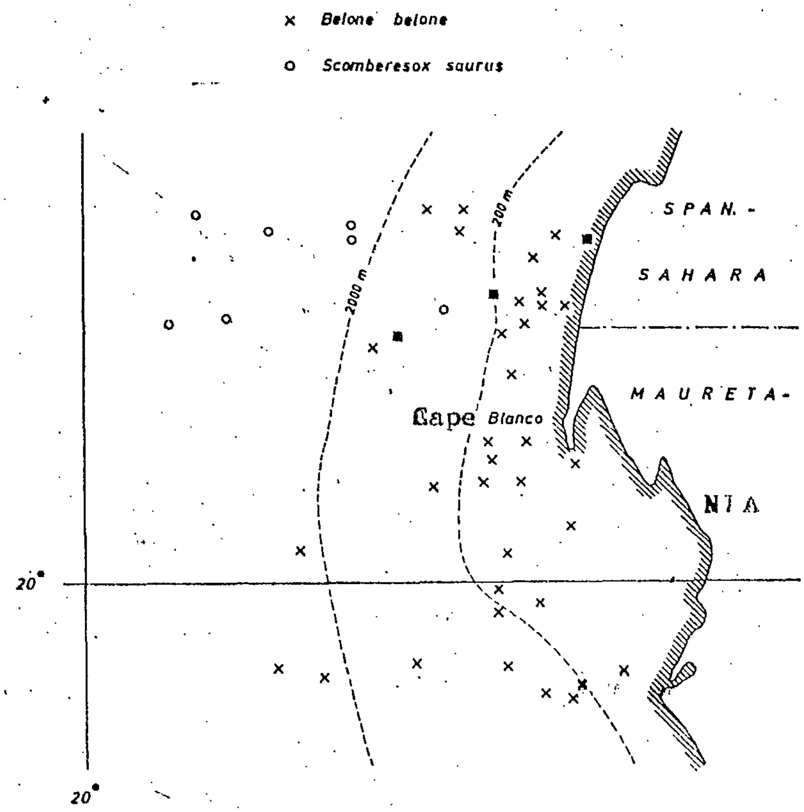


Fig. 23. Scomberesox saurus and Belone belone caught in pleustal layer (1968).

The second distribution factor is the temperature of the water. p. 46 cont'
In 1967, the water temperatures for the fishes from regions 1-5* lay between 17.3°C and 24°C, that is, the range of temperatures was very wide. For the fishes in the regions 4-5, however, the surface temperatures of the water stayed above 22.5°C. While 4 of the 5 species of this region p. 48
(4-5) were missing, perhaps because of the low spring temperatures (19.5-21°C) at the Great Meteor Seamount region during spring, the fish of regions Sp 5 and Su 1-3 avoided perhaps particularly the high temperatures

*Translator's note: possible printing error (1-3 ?) since this would be in contradiction to the next sentence in which seperate temperatures are mentioned for regions 4-5 which would be included in "1-5".

p.47

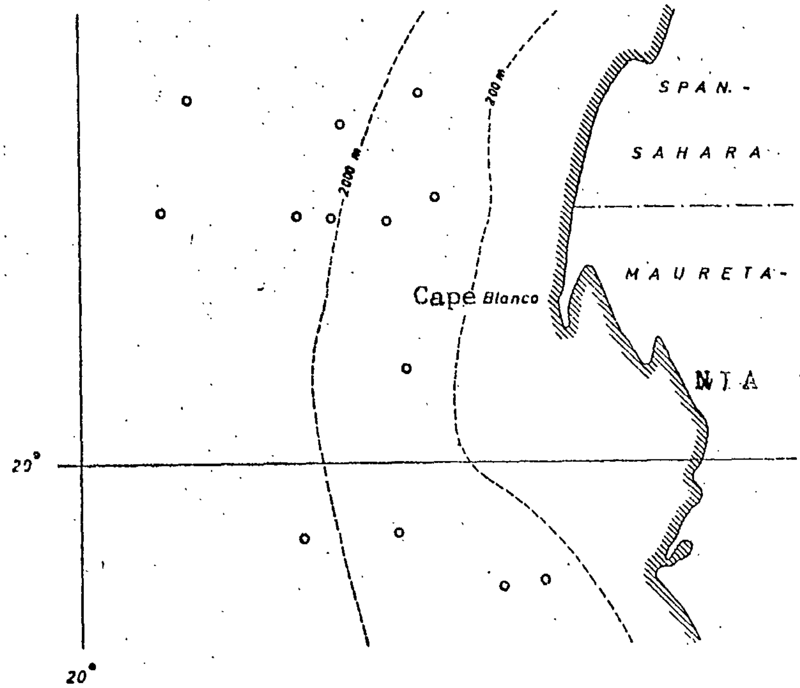
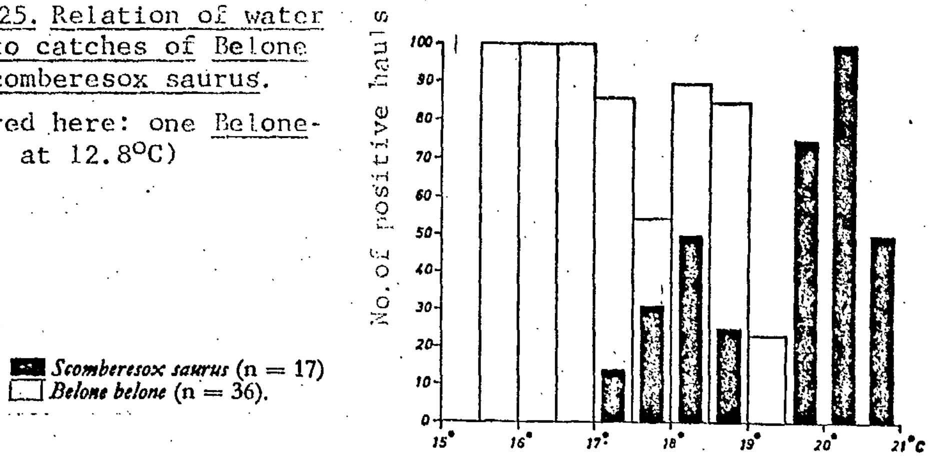


Fig. 24. Myctophidae caught in pleustal layer (1968).

Fig. 25. Relation of water temperature to catches of Belone belone and Scomberesox saurus.

(Not considered here: one Belone-positive haul at 12.8°C)



that prevailed during summer in the Great Meteor Seamount region. p.48 cont'd

The influence exerted by the water temperature upon the distribution of ichthyoneuston had been established also by BARTLETT & HAEDRICH (1968). They found, for example, along the Atlantic coast of SouthAmerica the larvae of **Makeira nigricans** only at surface temperatures above 25°C, and BACKUS et al. (1969) caught Gonichthys coccoi and Astronesthes niger almost exlusively or exclusively in the pleustal domain north of a temperature front in the Sargasso Sea.

The alternating distribution of Belone belone and Scomberesox saurus observed in our material emphasizes the important role played by the surface temperature of the water in curbing the distribution of species. In the case of both the species just mentioned, the distribution observed in the principal sampling area during the "Meteor" journey of 1968 is shown in Fig. 23 (p. 115). It shows that, of the 43 hauls in which one of the two related species was caught, only three hauls contained simultaneously Belone belone and Scomberesox saurus. It can be suspected that, in this extensive isolation of both these species from one another, water temperature plays a decisive role: While Belone belone (1967 and 1968) was limited to water temperatures between 12.8°C and 19.4°C , Scomberesox saurus was found in temperatures ranging from 17°C to >23°C. Generally, Belone belone thus preferred the lower temperatures.

The frequency of distribution of Belone-positive and Scomberesox-positive hauls to the individual temperature regions in 1968 is illustrated in Fig. 25 (p. 116). It shows a partial isolation of both species. Probably, besides water temperature, the distance to the mainland and the abundance of plankton in these waters also play a role in the distribution of Belone belone: Similarly to 1968, Belone belone was found also in 1967 only in upwelling waters (Fig. 22, region # 1 = 5 hauls; p. 113).

Paragraph 4.7 (p. 121) represents the regional distribution of Belone belone in connection with large-scale interrelations. In the following, the surface temperature of the water prevailing in the sampling regions will be discussed in regard to some of the species caught. It is of course possible that, in this respect, isolated, drifting fish cadavers may have falsified the picture. The values obtained should also not be generalized because various ecotypes can, as is known, have different tolerance limits.

In 1967 and 1968, Onos spec. was limited to regions with the lowest temperatures (11.6°C to 14.8°C). Low temperatures are tolerated, besides Belone belone, also by the myctophids Myctophum punctatum and Symbolophorus veranyi (12°C). Myctophum punctatum advances, according to BECKER (1967), in Atlantic waters all the way to Greenland.

Among the species that were not caught in waters with surface temperatures above 21°C, there were Onos spec., Belone belone (up to 19.4°C), the myctophids Symbolophorus veranyi (up to 19.6°C) and Hygophum hygoni (up to 21°C), Mugil spec. (up to 20.9°C), and Macrorhamphosus scolopax (up to 21°C).

However, according to BECKER (1967), the southern boundaries of distribution in the Atlantic start for Symbolophorus veranyi actually only with the 25°C summer isotherm.

In regions with temperatures above 21°C, the species caught were Scomberesox saurus, the four myctophids Myctophum punctatum, Myctophum nitidulum, Gonichthys coccoi and Hygophum hygomi, as well as Astronesthes niger.

4.62 Quantitative comparisons between regions and seasons

CLARKE (1940) observed on aneustonic zooplankton in the subtropical West-Atlantic, that density of catches diminished with advancing distance from the coast. He found, as an annual average, the ratio for coast / continental slope / ocean to be 16 / 4 / 1.

In analogy to this finding, DAVID (1965a) observed that oceanic catches were usually poorer than hauls in coastal or upwelling areas.

As for the method for the following comparisons of sample densities, there were always two series of samples compared with one another. The two series to be compared originated from different regions, but were obtained during the same or adjacent time intervals. (A 24-hr.-day was subdivided into 8 day and 8 night groups; cf. chapter 3, p.21.). The pair by pair comparison furnished the largest possible number of appreciable samples, which had to have been obtained during identical or adjacent time intervals so that the error, introduced by diurnal migration of the animals from both sample series, could possibly be eliminated. Since each of the five series of compared pairs consists of samples from different time intervals, the calculated values do not represent the absolute, but the relative abundance.

For an appraisal of the difference between ocean and shelf, 26 samples each were once compared, both series from the summer of 1967. The oceanic stations were located west of longitude 22° (samples 115-175), while the neritic stations were near the North-African/Portuguease coast (samples 45-70, regions # 1 and # 2 in Fig.22, p.113). The resulting ratio for the sample density was 576:811 = appr. 2:3, whereby the confidence limits of the means were overlapping.

19 samples each from Great Meteor Seamount / shelf, obtained in spring 1967 showed a relative abundance of (242:806) 1:3. p.49

In the three following appraisals there is always a plankton-poor region compared with a plankton-rich region.

For comparisons between the areas north and south of Cape Blanco, 19 samples each, taken in 1968, were utilized. The entire region is located between latitudes 22°30'N and 18°N and longitude 18°W. The location of the upwelling region at that time became apparent from the rough evaluation of the results of individual work teams obtained during "Meteor" cruise # 13: South of Cape Blanco was the center of the upwelling area; north of Cape Blanco certain manifestations of upwelling waters could still be observed but these became more and more weak in north-bound direction. According to this location of the upwelling area, different sample densities were to be expected from the areas north and south of Cape Blanco. There resulted still a relative abundance of (745:1955) appr. 1:2.5, but the confidence limits of the mean values were overlapping.

Furthermore, 21 samples each were compared from the Great Meteor Seamount region (taken in April 1967) and from the region of our actual assignment south of Cape Blanco (the boundaries of which were mentioned in the previous paragraph) sampled in May 1968. The resulting ratio was 257:2276 = 1:9. Here, the confidence limits do not overlap; however, if it is considered that the immersion of the neuston net was only about 10 cm in 1967, but 13 cm in 1968, the ratio decreases to 1:7.

Finally, 19 samples each were compared from the Great Meteor Seamount (spring) and from the region north of Cape Blanco. Here, the ratio for sample density was 176:837 or, upon taking the difference in net-immersion into consideration (see above), it was (246:837) 1:3.

Comparison of these regions reveals meaningful relations: The lowest sample density was found in the trophically poor region of the Great Meteor Seamount. More fishes were caught in 1967 along the Portuguese-African coast, and in 1968 in the upwelling fringe-regions. Finally, the greatest amount of fishes were caught in 1968 in the upwelling region south of Cape Blanco (the ratios were 1-3-3-7).

Seasonal fluctuations of ichthyoneuston have been investigated only by PENNELL (1967) in the boreal West Atlantic. The only neustonic species, Onos cimbrius, caught by PENNELL in the Gulf of Saint Lawrence was found only during summer. Perhaps, seasonal migration of ichthyoneuston in subtropical regions is similar to that described by SHOJIMA (1964) for Sargasso fish, namely that qualitative and quantitative composition undergoes seasonal changes, and that the fish is found less frequently during winter.

In the region of the Great Meteor Seamount, material was collected in 1967 during spring and summer. Upon comparing the species of this region from April with those from June/July, it becomes apparent that four species (Macrorhamphosus scolopax, Danichthys rondeletii, Phycis phycis, and Hygophum hygomi) were caught exclusively in spring, and six species (3 Exocoetidae, Coryphaena hippurus, Coryphaena equiseiis, and Nealotus tripes) exclusively during summer. This may be due to the seasonal fluctiation in the temperatures of the water.

The spring/summer ratio of the sample density of fishes from the Great Meteor Seamount was calculated from the total number of fishes in the 30 samples each from April and from June/July. The resulting ratio was 359:536 = 2:3. The mean values from both series show no statistically significant difference. Therefore, as was expected, seasonal fluctiation was not demonstrable on our material.

4.7 On the ecology of ichthyoneuston

The general ecology of the pleuston has been outlined by ZAITSEV (1968). However, the distinct ecology of the ichthyoneuston requires special attention.

Chapter 4.2 (p. 27) emphasizes the biological distinction of the 0-15 cm level from the adjacent microlayers in quantitative as well as qualitative respects, and shows at the same time that the population density of the pleuston stayed behind that of the 0-30 m macrolayer. This distribution poses the question as to the ecological correlations.

The basic problem dealt with in this chapter should be summarized as follows: The distinctive physical conditions prevent a normal population density in the uppermost centimeters of the ocean. On the other hand, this particular layer offers certain advantages to adapted species.

Factors adverse to life in the pleuston shall be mentioned first: The uppermost centimeters of the ocean are marked by strong undulations and extreme fluctuations in salinity and temperature. Dashing waves[5] disturb first of all the youngest stages. While older fishes stay in their biotope even if waves rise to 3 and 4 m, fish eggs can be dispersed and killed commencing at force 3 winds (ZAITSEV 1968). An influence by wave motion upon vertical distribution of fishes was suspected also by ZUSSER (1956). He believed that, among other factors, the quieter hydro- p. 5
logical conditions in the deep sea entice fishes participating in vertical migration to leave the surface in the morning for deeper strata.

Important for life at the surface is, furthermore, the intensive radiation. Characteristic for the pleustal domain is the extensive absorption of infrared radiation (JERLOV 1968). HERRING (1965 and 1969) considers for example the pigmentation of a copepod and an isopod from the pleustal layer as a protection against radiation. Juvenile fishes

---

5) T. POMMERANZ is preparing his thesis on the influence of wave forces and radiation upon fish eggs, at the Institute for Oceanography, Kiel, Germany.

are protected by melanin or, like the copepoda Pontella atlantica, Pontella lobiancoi, and Anomalocera p., by silvery (guanin ?), reflecting backs (Liza aurata, ZAITSEV 1961; Belone belone). However, it is the youngest stages that are endangered, also because of their relatively large superficies. MARINARO (1966) established experimentally that solar radiation can kill fish eggs, DANNEVIG & SIVERTSEN (1933) showed that radiation does harm larvae.

Diurnal distribution (three times as many fishes by night than by day; cf. Fig.6, p.30), and the noon-time descent (Fig.5, p.29) are to be considered as a reaction to extreme conditions of radiation.

The intensive illumination must be an additional negative factor for every potential prey among the fishes of the pleuston because, in the light, the fish is easier spotted by its enemy. The surface-negative vertical distribution of eggs and larvae in the Atlantic pleuston (Fig.9, p.40) is perhaps to be interpreted as an adaptation to the stronger moving waves, radiation, and the observability in the light at the surface of the ocean; also, extreme radiation and wave conditions may perhaps permit the most successful neuston species to migrate into the 0-15 cm layer only at a length of about 6 mm (cf. 4.4, p.53).

After discussing the factors adverse to life in the pleustal domain (dashing waves, radiation, predators), the question of food supply for ichthyoneuston shall now be dealt with. In this connection, the microbiology and especially the phosphate striation of the pleuston should be mentioned which was investigated by GOERING & WALLEN (1967):

They found the highest concentration of phosphate above the leap zone, often in the uppermost 50 cm, and even at wind forces 2-4 (Beaufort scale) was the characteristic phosphate stratification in the uppermost 50 cm preserved. Such a degree of stability of the phosphate stratification points to a minimum of whirl in the surface water; this is perhaps the prerequisite for the existence of small organisms at the surface.

Important to the microorganisms in the pleuston could be, in addition, the high concentrations found in the surface film of particulate and solute organic carbon, nitrogen and phosphorus, nitrate and phosphate (WILLIAMS 1967). These substances could perhaps furnish the nutritive basis for the organisms in the surface film (NORIS unpublished, after CASSIE 1963, HARVEY 1966), and in the pleuston. However, it is not certain whether the microfauna of the oceanic pleuston is equally abundant as that of the pleuston in the Black Sea (ZAITSEV 1961, TSIBAN 1967, and MOROZOVSKAYA 1966 — after ZAITSEV 1968). In any event, a great number of observations point to the food shortage for pleuston fishes; the preceding chapters illustrated the heterogeneity of ichthyoneuston in regard to: Diurnal migration (4.3, p.42), seasonal migration (4.62, p.118), horizontal distribution as dependent upon water temperature and depth (4.61, p.112), vertical distribution (4.22, p.37), feeding rhythms (4.53, p.84), types and size of food objects ((4.54, p.93). As a consequence of this heterogeneity, there was only an average of 2.3 fish groups caught per top-net haul, and in 1968 only an average of 2.7 of the fish groups listed in Table 5 (p.25). This minimal number of species per haul could be interpreted as follows: The food shortage of the surface layer does not permit a larger number of directly competing species at the pleustal level because spreading of the food potential to include more consumers would endanger the continuity of those particular species whose life patterns are gauged especially to the pleuston.

A number of additional phenomena, which have in part been discussed before under the appropriate headings, all point to the food shortage in the pleustal domain:

The result of only one neustonic invertebrate and only a single fish species in the Gulf of Saint Lawrence (PENNELL 1967 — catching device Table 1, p. 11); the poorer catches (wet weight of total haul) in the pleustal layer of the North Sea (HEMPEL & NELLEN 1969) as compared to the 0-60 m macrolayer (Gulf III, oblique haul); the low sample density of fishes caught at the 0-15 cm level in contrast to the 0-30 m macrolayer sampled with the larvae net (4.213, p.35); the dominance of juveniles in the pleustal domain as a convergency phenomenon mimicking dwarf fauna of sargasso weed (4.4, p.57); the exiguous number of food specialists (4.522, pp. 79-80), and the homogeneity of stomach contents (4.541, p.93); the indiscriminate consumption of food (Figs. 12s, 12t; p.67); finally, the fact that especially the Myctophidae (besides Belone belone the most massive neuston fish; see below) supplement their food in the subpleustal layers (Fig. 19, p.92), and that particularly two of the smallest (Table 5, p.25) Myctophidae are markedly surface-positive (Table 6, p.39).

Some observations indicate that in the pleustal domain, plankton scarcity is especially pronounced by day:

In 1967, the day/night ratio (time limits 2-7/10-15) for the sample density of fishes caught at the 0-10 cm level (4.21, p.27) was 1:3 (Fig. 6, p.30). p.5'

The day/night ratio for the number of species (groups mentioned in Table 5, p.29) per haul from the 0-15 cm layer was, in 1967, 1:2 namely (108:68):(173:56).

By day, aggregations (4.36, p.50) and larger stages (4.4, p.52) were largely missing from the pleuston. Even the only oceanic cephalopod which lives, according to CLARKE (1966) as an adult at the surface also by day, the blue-pigmented (as many neustonic fish are) Onychia carribaea, represented as a juvenile in our samples (Hartmann 1970 a) reaches only a mantle length of 36 mm (CLARKE 1966).

Finally, the intestinal contents of fishes feeding in the pleustal layer by day show an especially marked similarity (4.54, p.93).

The food shortage could be interpreted as a consequence of the distinct physical conditions in the pleustal domain.

It seems that more favorable food conditions prevailed in the pleustal layer of the upwelling regions than in the rest of the area sampled. The indicative factors for this are: The high density of the samples from the upwelling region (1968) (4.62, p.118), and the distribution of Belone belone (4.61, p.112) in connection with its maximal size which is unusual for ichthyoneuston, and its diurnal rhythm which is equally unusual for older neuston fishes (4.31, p.42).

Belone belone up to 370 mm (measured from the anterior rim of the eye to the tip of the caudal fin) was limited, in 1967 as well as 1968, to the upwelling regions and their fringe-areas (4.61, p.112). At the same time, Belone belone distributed the largest among the fishes caught with the neuston net: 29 animals between 80 mm and $>$370 mm; unusual is furthermore that Belone belone remains in the pleustal layer by day even with its older stages. This distinct behavior of Belone belone with respect to diurnal migration, ontogenetic vertical movement, and horizontal distribution can be perceived as the consequence of an increased food supply in the pleustal layer of the upwelling regions: In the upwelling region alone, and here even by day, the abundance of food made the existence of such large neuston fishes possible.

Therefore, food shortage seems to exist for fishes particularly by day in the pleuston of the open ocean which is devoid of upwelling waters.

While the observations cited indicate a regional food shortage in the pleustal layer, a multitude of invertebrates and fishes live, according to ZAITSEV (1961, 1968) in the uppermost 5 cm of the Black Sea, exceeding otherwise known concentrations considerably. This discrepancy between the results from the Black Sea and the Atlantic Ocean may, in part, be due to the fact that the microlayers sampled were of different thickness (5 cm/15 cm). Nevertheless, it seems that different conditions exist in the ocean than in the Black Sea which is known to have its own special hydrographic conditions. While, according to ZAITSEV (1961) the bulk of pelagic eggs and fish larvae of the Black Sea develops in the 0-5 cm layer, the first fish stages occurred in the Atlantic pleuston in fewer numbers than in deeper microlayers (Fig. 9, p. 40). The accumulation of juveniles also finds, according to ZAITSEV, "abundant food" in the 0-5 cm layer of the Black Sea, and finally, the plankton concentrations in the 0-5 cm layer of the Black Sea attract the adult fishes. By contrast, the number of individuals of all stages remained low in the Atlantic pleuston. Therefore, the pleustal layer of the subtropical NE Atlantic (0-15 cm) has an inferior capacity as a grazing-ground for fishes to that of the Black Sea (0-5 cm).

It seems therefore that generalizations (ZAITSEV 1968: La Neustonologie marine) especially with regard to the important problem of food supply for ichthyoneuston would be premature.

Having discussed the factors adverse to life as well as their effects, factors that are favorable for fish shall be summarized.

A special source of nourishment in the pleuston is seen by ZAITSEV in the upwelling, decaying plankton cadavers as they were found by ZELEZINSKAYA (1966) in the Black Sea after ZAITSEV. In this connection, it should be mentioned that the "Meteor" neuston samples occasionally contained considerable amounts of exuviae.

The favorable light conditions in the pleuston serve not only the predator but also the visually guided plankton grazer: The fact that the most light is needed for spotting the smallest objects agrees with the observation that the smallest stages feed in the pleustal layer by day (Fig. 19, p. 92), while, generally, the medium stages prefer feeding by night in the then less illuminated but plankton-richer pleuston (4.533, p. 86). Still longer fishes finally, are probably least dependent upon illumination of the cover layer because of the size of their prey and, as shown in chapter 4.4 (p. 52), many species leave the pleustal domain upon having reached puberty to feed then in perhaps nutritionally richer, but weaker illuminated, deeper strata.

The fact that some neuston fishes are an exception to the rule (ZUSSER 1956) that planktotrophic pelagic fishes do not feed by night, but during dusk/dawn or by day (4.533, p. 86), can probably also be related to the special light conditions in the pleustal domain. Interestingly enough, <u>Astronesthes niger</u> (Table 7, p. 43) who appears in the pleustal layer only around midnight and is conspicuous also because of the smallness of his eyes, does not seem to ingest any food while visiting the pleuston.

The importance of illumination is emphasized also by the discrepancy between the distribution of invertebrates and of fish. Although the plankton density was more pronounced, by night and during dusk/dawn, in the 15-30 cm layer than in the layer above (WEIKERT, oral communication), nine frequent fish species (Fig. 9, p. 40) were roaming predominantly within the uppermost 15 cm. The same tendency was observed in the boreal domain (HEMPEL 1970).

The uppermost level provides, next to favorable trophic conditions, despite the illumination of the biotope also a relative protection against aquatic enemies because the fish who migrates into the uppermost centimeters thus decreases the target area for an attack by the swimming enemy: Here, "he stays with his back to the wall", so to speak. This hypothesis finds support in the well-known flight behavior of some surface fishes such as the Exocoetidae, and Scomberesox saurus (LEIM 1966) who, pursued by predators, even leave the water in their upward escape. Ichthyoneuston that escapes below the water surface is mentioned in chapter 2.2 (p. 13). The surface represents probably a relatively protected niche especially for those fishes that do not ingest food during their stay in the neustonic layer (4.53, p. 84). However, since pleuston fishes get into the reach of neustonic predators (brachyura, isopoda) and of birds (4.541, p. 105), the advantage of this peripheral environment is again diminished.

However, since, despite the advantages offered by the pleustal domain as a trophical niche and temporary habitat, the macrolayer of 0-30 m is populated by at least 1.65 times more fishes (4.213, p. 35), it is obvious from this ratio that special factors characteristic for the pleuston, but adverse to life, such as the dashing of the waves, radiation, and predators which hinder normal population of the biotope, exert a greater influence than the favorable factors such as good visibility of the food, "anticadaver-rain", and peripheral position.

Then again, their low number offers another advantage to the ichthyoneuston, namely, if population density in the pleustal domain remains so low that it is not worthwhile for some predators to hunt the ichthyoneuston, this diminishes for the potential victim the danger to be devoured.

Interestingly enough, KRISTENSEN (1964) described another trophically poor peripheral biotope, the hypersaline bays of Curaçao, as an environment for young stages (Mugil, Atherina, Elops, Harengula, among others). There too, some of the factors mentioned may be of ecological importance. However, in these bays, additional organic components of the water, not yet analyzed, seem to be an important factor to these fishes (KRISTENSEN 1964).

Summary*

The marine ichthyoneuston populates the free waters of the cover-layer of the pelagial, that is, the uppermost 15 cm known as the pleustal domain. Subject of this work is the hypothesis that the pleuston in the horse-latitude region of the open Atlantic, although nutritionally poor, represents a relatively plankton-rich pasture for the fish fry. The distribution of the fishes from the pleustal layer has been included in this investigation.

The sampling device — a modified neuston glider, after DAVID — was towed during a standard haul for 30 minutes at a speed of 6 knots. It fished with a net-opening of 30 x 15 cm at the level of appr. 0-10 cm, and

*) Translator's note: Although an English summary is provided with the original text, it was found to be incomplete and somewhat awkward in its formulation; therefore a translation of the German "Zusammenfassung" is herewith provided.

with an additional net of equal size, in most cases simultaneously, one of these three microlayers: appr. 10-25 cm, 23-38 cm, 38-53 cm. The mesh sizes used were 300 μ and 500 μ. The bulk of the material, consisting of 354 samples, was obtained in 1967 by the research vessel "F.S. Meteor" in the predominantly nutrient-poor region between the Great Meteor Seamount (30°N 28°30'W), and the Portuguese-Moroccan coast; and in 1968, the material was supplemented by 123 samples collected by the "Meteor" in the nutritionally rich region of the upwelling waters off Mauretania.

Between the results from 1967 and 1968, no contradictions arose.

34 groups of fish (different taxa) were found in at least three of the 262 hauls from the 0-10 cm level. Predominant were the beloneforms with 8 and the Myctophidae with 9 species. The most frequently found species were:

(1) *Scomberesox saurus* (6—136 mm total length) 162 hauls
(2) *Gonichthys coccoi* (17—61 mm total length) 62 hauls
(3) *Belone belone* (8—370 mm total length minus snout) 40 hauls

The most frequent lengths were between 6 to 80 mm.

The majority of neuston fishes limited their presence in the pleustal domain to a certain time of day, as follows:

(1) by day and night:
Mugil spec. (7—63 mm)
Coryphaena equiselis (10—40 mm)
a Berycid (6—17 mm)
larvae of Clupeoidae (16—30 mm)
Belone belone (8— > 370 mm)
small *Scomberesox saurus* (6—29 mm)
(2) in the daytime
Macrorhamphosus scolopax (7—69 mm)
small Exocoetidae (± 6—20 mm)
(3) at night
larger *Scomberesox saurus* (50—136 mm)
larger Exocoetidae (± 20—70 mm)
Trachurus spec. (15—56 mm)
juvenile and adult Myctophidae

(4) especially at dusk and dawn
larvae of Myctophidae
(5) about midnight
Astronesthes niger

p. 53

Of the groups inhabiting the pleustal domain by day, those rich in numbers did, as a rule, not migrate into deeper layers in contrast to groups numbering fewer individuals. In the diurnal rhythm of the ichthyoneuston on the whole, a midnight and a noontime descend could be observed. Fishes caught by day were mostly few in numbers and smaller than the night-positive species or stages. The top-net catches were richer than those from the middle or lower nets. In 1967 the sample density per 160 m^3 water of the three microlayers covered were:

	by day	dusk/dawn	by night
0-10 cm	7	17	23
10-25 cm	1	12	4
38-53 cm	2	1	2

In the 0-30 m layer which was fished with a Helgoland larvae net equipped with alternating bucket mechanism, the sample density was statistically significant 1.65 times higher than at the 0-10 cm level. Radiation, illumination, dashing waves, and specializing predators probably prevent a higher population density in the pleuston.

The vertical distribution of species within the uppermost 60 cm showed three patterns of behavior:

1) surface-negative = first developmental stages (3 groups)
2) slightly surface-positive ≙ Myctophidae (4 groups)
3) strongly surface-positive = Myctophidae and others (9 groups)

The horizontal distribution of the neustonic species is determined by water depth, surface temperature, and food supply. In 1967, sample density in the three microlayers reached at 0-10 cm = 15, 10-25 cm = 5, and at 38-53 cm = 2 fishes per 160 m^2. Upwelling plankton cadavers, illumination, microfauna, and peripheral location of the biotope may be causative factors for the greater density of ichthyoneuston at the 0-10 cm level.

The density of samples from the following regions were compared:

1) Great Meteor Seamount, April 1967
2) Great Meteor Seamount, June-July 1967
3) African-Portuguese shelf, 1967
4) fringe-region of upwelling area north of Cape Blanco, 1968
5) upwelling region south of Cape Blanco, 1968

This list comprises regions whose waters differ in part vastly as regards nutritional contents. Corresponding differences were apparent also among relative sample densities; here, the values were 1-1-3-3-7. These proportions are statistically not significant.

Generally, the neuston samples represented merely the average proportions from the length-range of the species: The lower limit of the total length of fishes that stay in the pleustal domain by day was for nine species 6 or 7 mm. The majority, especially among day-positive ichthyoneuston, were juveniles, a convergency phenomenon imitating the dwarf fauna of drifting Sargasso weed. About half of the 463 Gonichthys coccoi collected in 62 hauls measured 22-25 mm. According to the characteristic intestinal contents from 693 animals, four developmental stages could be determined in Scomberesox saurus based on their diet:

1) protozoa-gastropoda age (6-15 mm)
2) gastropoda-entomostraca age (16-30 mm)
3) entomostraca age (31-45 mm)
4) crustacea age (46-113 mm)

Characteristic contents of the digestive tracts were:

1) fish, feeding on neuston by day only: large amounts of cladocera;
2) small stages feeding on neuston by day only: large amounts of mollusks;
3) large fish, feeding on neuston by day only: large amounts of Corycaeus, isolated Sapphirina;

4) larger ichthyoneuston: ostracoda;
5) fish, not feeding on neuston by day: amphipoda.

It could be shown on Scomberesox saurus, Macrorhamphosus scolopax, and the myctophid Gonichthys coccoi, on hand of a cross-section from the length-range of the atlantids that had served as their food, that the length spectrum broadened with increasing fish length and shifted toward the larger gastropoda shells. The larger fishes no longer fed on the smallest gastropoda.

Similarly composed intestinal contents were found in each of the following principal ichthyoneuston groups:

1) small fish, feeding exclusively on neuston and only by day;
2) larger fish, feeding exlusively on neuston and only by day;
3) fish that do not feed on neuston by day.

Hereby, each of the three principal groups was composed of 4-5 species or developmental stages. The degree of competition for food was calculated on hand of 78 pairs of species or stages on the basis of frequency and amount of the eight most important trophical animals. High degrees of competition for food existed within the groups feeding on neuston by day, a lower degree of competition was found within the heterogenic groups of fishes not feeding on neuston during day, and especially between these and the small stages feeding on neuston by day. In addition, from the overlapping of length-ranges of the consumed atlantids (see above), the degree of competition for food was calculated for 21 pairs from the p. 54
length groups of three species (see above). In each case the individual values of the pairs, calculated as indices for the food competition between the length groups, once on the basis of the food type, then from the size of consumed atlantids, correlated positive with r = 0.70 (95% confid. $0.32 \leqq \varrho \leqq 0.85$.

On the basis of time of day and depth level at which the food was consumed, 4 groups were distinguishable from the contents of the digestive tracts. Food was ingested

1) in the pleustal layer by day only:
   smaller Scomberesox saurus (6-45 mm)
   Exocoetus obtusirostris (6-33 mm)
   Macrorhamphosus scolopax (8-50 mm)
   one berycid (6-17 mm)
   Coryphaena equiselis (10-40 mm)

2) during vertical movement in subpleustal strata and probably in pleustal layer by night:
   larger Scomberesox saurus (50-113 mm)

3) by day in subpleustal strata and in the pleustal layer by night:
   7 species of the Myctophidae family

4) only (?) by day in subpleustal strata:
   Trachurus spec.

As indices for food shortage in the pleustal domain of the open subtropical NE Atlantic may be considered:

1) The variety of distribution patterns; only 2.3 of the 31 groups found most frequently were caught in 1967 per 160 m^3 at the 0-10 cm level;

2) the low sample density as compared to the 0-30 m macrolayer;

3) the dominance of juveniles — a convergency phenomenon toward the nanism of sargasso fauna;

4) the exigous number of food specialists and the homogeneity of stomach contents;

5) the indiscriminating food intake;

6) food-intake of Myctophidae, the most massive neuston fishes, which is therefore supplemented by feeding in subpleustals strata to compensate for the food shortage in the areas sampled;

7) the low maximal length especially of the two "markedly surface-positive" Myctophydae species.

The following observations indicate that food supply is particularly short in the pleustal domain by day:

1 and 2) The day/night ratio of sample density with regard to individual fishes caught was 1:3, with regard to fish groups it was 1:2;

3 and 4) aggregations as well as larger fishes were missing except for Belone belone (see below).

5) intestinal contents, particularly of fishes feeding in the pleustal layer by day, showed a strong similarity in regard to type, amount, and size of food object.

On the other hand, in upwelling waters, more favorable food conditions seem to have existed than in the remaining regions sampled. This is indicated by

1) the higher sample density for fishes from the upwelling region (1968);

2) the distribution of Belone belone which was limited in 1967 as well as 1968 to the upwelling regions, in connection with the fact that Belone belone was an exception to the rule not only by its maximum size but also by its older stages which remained at the surface even by day.

Literature

p. 56

1. Aboussouan, A. (1965): Oefs et larves de Teléostéens de l'Ouest africain. II Distribution verticale. —Bull. Inst. français d'Afrique noire, Sér. A, Sci. nat. 27, 4, 1504—1521.
2. Aron, W. (1962): Some aspects of sampling the macroplankton. — Cons. perm. int. Expl. Mer, Rapp. et Proc.-Verb. 153, 5, 29—38.
3. Aron, W. & Collard, S. (1969): A study of the influence of net speed on catch. — Limnol. and Oceanogr. 14, 2, 242—249.
4. Aschoff, J. & Wever, R. (1962): Beginn und Ende der täglichen Aktivität freilebender Vögel. — J. Ornith. 103, 2—27.
5. Assmann, A. V. (1957): Microorganismen als Nahrung für Jungfische. — (Russ.), Zoologiceskij Zhurn. 36, 6, 900—908.
6. Backus, R. H., Craddock, J. E., Haedrich, R. L. & Shores, D. L. (1969): Mesopelagic fishes and thermal fronts in the western Sargasso Sea. — Mar. Biol. 3, 2, 87—106.
7. Baker, A. de C. (1960): Observations of squid at the surface in the N E Atlantic. — Deep-Sea Res. 6, 206—210.
8. Balech, E. (1959): Tintinnoinea del Mediterraneo. — Trab. Inst. Esp. Oceanogr. 28, 1—88.
9. Banse, K. (1964): On the vertical distribution of zooplankton in the sea. — Progress in Oceanography, M. Sears (Ed.) 2, 53—125.
10. Bartlett, M. R. & Haedrich, R. L. (1968): Neuston nets and South Atlantic larval Blue Marlin (*Makaira nigricans*). — Copeia 3, 469—474.

11. BECKER, V. E. (1967): Die Myctophiden der „Petr Lebedev"-Atlantikexpeditionen 1961—1964, (Russ.): — Trudy Inst. okeanol. (Moskva) 84, 84—124.

12. BEN-YAMI, M., HERZBERG, A., PISANTY, S. & LORIE, A. (M. S.): A side-tracking neuston net. (Ms.) — Sea Fish. Res. Station — Haifa, Israel, 1—13.

13. BIERI, R. & NEWBURY, T. (1966): Booby II, a quantitative neuston sampler for use from small boats. — Publ. Seto Mar. Biol. Lab. 13, 5, 405—410.

14. BIGELOW, H. B. & SCHROEDER, W. C. (1953): Fishes of the Gulf of Maine. — Fish. Bull. Fish Wildl. Serv. U. S. 53, 74, 577 pp.

15. BOGOROV, B. G. (1958): Perspectives in the study of seasonal changes of plankton and of the number of generations at different latitudes. — In: Perspectives in Marine Biology, ed. A. A. BUZZATI-TRAVERSO, 145—158.

16. BOGUSLAVSKY, S. (1956): Die Absorption der Sonnenstrahlung im Meer und ihr direkter Einfluß auf die Wassertemperatur (Russ.). — Arb. a. d. Meeres-Hydrophys. Inst. 8 80—97.

17. BOLCHAKOV, V. (1963): Etude de l'hydrologie de la couche supérieure á 1 mêtre d'eau en Mer Noire. — Notes Sci. Station biol. Odessa (en ukrainien) (nicht gesehen) 5, 63—69.

18. BOLIN, R. (1959): Iniomi Myctophidae. — Rep. on the Sci. Results of the "Michael Sars" North Atlantic Deep-Sea Exped. 1910, 4, 2, 7, 1—45.

19. BREDER, C. M. (1962): On the significance of transparency in osteichthid fish eggs and larvae. — Copeia 3, 561—567.

20. BRIDGER, J. P. (1956): On day and night variation in catches of fish larvae. — J. Cons. perm. int. Expl. Mer 22, 42—57.

21. BROCK, V. E. & RIFFENBURGH, R. H. (1960): Fish schooling: a possible factor in reducing predation. — J. Cons. perm. int. Expl. Mer 25, 3, 307—317.

22. BRUUN, A. F. (1935): Flying-Fishes (Exocoetidae) of the Atlantic. — Dana-Rep. 6.

23. CASSIE, R. M. (1959): Micro-distribution of plankton. — N. Zealand J. Sci. 2, 398—409.

24. — (1963): Microdistribution of plankton. — Oceanogr. Mar. Biol. Ann. Rev. 1, 223—252.

25. CLARKE, G. (1940): Comparative richness of zooplankton in coastal and offshore areas of the Atlantic. — Woods Hole Coll. Repr. 241, 226—255.

26. CLARKE, M. R. (1966): A review of the systematics and ecology of oceanic squids. — Adv. mar. Biol. 4, 91—300.

27. CLOSS, H., DIETRICH, G., HEMPEL, G., SCHOTT, W. & SEIBOLD, E. (1969): „Atlantische Kuppenfahrten 1967" mit dem Forschungsschiff „Meteor" — Reisebericht. — „Meteor"-Forschungsergebn. A 5, 1—71.

28. COVILL, R. W. (1959): Food and feeding habits of larvae and postlarvae of *Ammodytes americanus* 1952—1955. — Bull. Bingham Oceanogr. Coll. 17, 1, 125—146.

29. CRADDOCK, J. E. (1969): Neuston fishing. — Oceanus 15, 1, 10—12. p. 57

30. CUSHING, D. H. (1951): The vertical migration of planktonic Crustacea. — Biol. Rev. 26, 2, 158—192.

31. D'ANCONA, U. et al. (1931—1956): Uova, larve e stadi giovanili di Teleostei. — Fauna Flora Napoli Monogr. 38.

32. DANIELSEN, D. S. & TVEITE, S. (1968): Sildelarver i overflatelaget ved Trøndelagkysten 1 april 1968. — Fiskets Gang 40, 692—694.

33. DANNEVIG, A. & G. (1950): Factors affecting the survival of fish larvae. — J. Cons. perm. int. Expl. Mer 16, 2, 211—215.

34. DANNEVIG, A. & SIVERTSEN, E. (1933): On the influence of various physical factors on cod larvae ..., J. Cons. perm. int. Expl. Mer 8, 1, 90—99.

35. DARNELL, R. M. & MEIERROTTO, R. R. (1965): Diurnal periodicity in the Black Bullhead, L. *Ictalurus melas* (Rafinesque). — Transact. Amer. Fish. Soc. 94, 1, 1—8.

36. DAVID, P. M. (1965a): The neuston net. A device for sampling the surface fauna of the ocean. — J. mar. biol. Assoc. U. K. 45, 313—320.

37. — (1965b): Die Fauna der Meeresoberfläche. — Endeavour 24, 92, 95—100.

38. — (1967): Illustrations of Oceanic Neuston. — In: Aspects of Mar. Zool., Symp. Zool. Soc. London 19, 211—213.

39. — (1968): Pelagic organisms in the superficial layers. — In: Sympos. on Antarct. Oceanogr. Santiago, Chile 13—16. Sept. 1966, Cambridge Scott Polar Res. Inst. 24—29.

40. DECHNIK, T. V. & SININKOVA, V. J. (1964): Die Verteilung von pelagischen Fischeiern und -larven im Mittelmeer (Russ.). — Trudy Sevastopol Biol. Stat. 7, 77—115.

41. DELLA CROCE, N. (1962): Aspects of microdistribution of the zooplankton. — Cons. perm. int. Expl. Mer. Rapp. et Proc.-Verb. 153, 25, 149—151.

42. DUNCKER, G. (1960): Die Fische der Nordmark. — Hamburg.

43. EHRENBAUM, E. (1905): Eier und Larven von Fischen. — In: Nordisches Plankton Zool. Teil 1. — Kiel u. Leipzig.

44. ELLIOTT, J. M. (1967): Invertebrate drift in a Dartmoor stream. — Arch. Hydrobiol. 63, 2, 202—237.

45. Faune Ichthyologique de l'Atlantique Nord (1929 ff.) hg. L. JOUBIN. — Cons. perm. int. Expl. Mer, Kopenhagen o. S.

46. FENAUX, R. (1968): Un dispositiv pour pêches planctoniques dans les couches superficielles. — Rapp. Comm. int. Mer Médit. 19, 3, 379—381.

47. Fiches d'Identification des Oefs et Larves de Poissons, (1965ff.): ed. J. H. FRASER et B. J. MUUS. — Cons. perm. int. Expl. Mer.

48. FOWLER, H. (1936): The marine fishes of West Africa. — Bull. Amer. Mus. N. H. 70 (2 Vols.) New York.

49. FRASER, J. (1962): Nature adrift. — G. T. Foulis & Co., London.

50. FRASER-BRUNNER, A. (1949): A classification of the fishes of the family Myctophidae. — Proc. Zool. Soc. London 118, 4, 1019—1106.

51. FRIEDRICH, H. (1965): Meeresbiologie. — Gebr. Borntraeger, Berlin: 436 pp.

52. FRYER, G. (1955): Scale-eating habits of African Cichlid fishes. — Nature 175, 1089—1090.

53. GHIRARDELLI, E. (1966): L'iponeuston del Golfo di Trieste. Metodi di raccolta primi risultati. — Boll. Zool. 33, 221—222.

54. GIBBS jr. R. H. & COLETTE, B. B. (1959): On the identification, distribution, and biology of the Dolphins, *Coryphaena hippurus* and *C. equiselis*. — Bull. Mar. Sci. Gulf Caribb. 9, 2, 117—152.

55. GOERING, J. J. & WALLEN, D. (1967): The vertical distribution of phosphate and nitrite in the upper one-half meter of the southeast Pacific Ocean. — Deep-Sea Res. 14, 1, 29—33.

56. HAGMEIER, A. & KÜNNE, C. (1950): Die Nahrung der Meerestiere. — In: Handbuch der Seefischerei Nordeuropas. 1, 5, a Schweizerbart, Stuttgart.

57. HARDY, A. & GUNTHER, E. (1935): Plankton and rough weather. — Discovery Rep. 11, 268—272.

58. HARTMANN, G. F. (1958): Mouth size and food size in young rainbow trout, *Salmo gairdneri.* — Copeia 3, 233—234.

59. HARTMANN, J. (1969a): Verteilung und Nahrung des Ichthyoneuston im subtropischen Nordostatlantik. — Diss. Math. Nat. Fak., Univ. Kiel: 218 pp.

60. — (1969b): Chalimusstadien von *Lepeophtheirus* auf juvenilen *Onos cimbrius* und *Onos mustelus.* — Ber. Dt. Wiss. Komm. Meeresforsch. NF 20, 2, 172—175.

61. — (1970a): Tagesgang und vertikale Mikroverteilung von Cephalopoden des Neuston westlich von Madeira. — Ber. Dt. Wiss. Komm. Meeresforsch. NF 21, ~~im Druck~~.

62. — (1970b): Juvenile Saury Pike (*Scomberesox saurus* WALB.), an example of ichthyoneuston. — J. Cons. perm. int. Expl. Mer 33, 2.

63. —: Bindung eines Neustonfisches an die Meeresoberfläche — Verhalten von juvenilen *Liza aurata* im Arenabecken und im Habitat.-Int. Rev. ges. Hydrobiol. (im Druck).

64. —: Verhalten von Neuston im Arenabecken. — (in Vorbereitung).

65. HARTMANN, J. & SCHNACK, D. (1969): Verteilung von Heringslarven und Plankton am 28. 5. 1969 in der Schlei: Absetzvolumen. Ber. Dt. Wiss. Komm. Meeresforsch. NF 20, 3—4, 288—296.

66. HARTMANN, J. & WEIKERT, H. (1969): Tagesgang eines Myctophiden (Pisces) und zweier von ihm gefressener Mollusken des Neuston. — Kieler Meeresforsch. 25, 2, 328—330.

67. HARVEY, G. W. (1966): Microlayer collection from the seasurface: A new method and initial results. — Limnol. and Oceanogr. 11, 4, 608—613.

68. HASLE, G. R. (1950): Phototactic vertical migration in marine dinoflagellates. — Oikos 2, 162—175.

69. HEMPEL, G. (1970): Distributional and trophic relationships of neuston and plankton. — [Paper of] IABO Symp., Tokyo, 20 pp.

70. HEMPEL, G. & NELLEN, W. (1969): Ichthyoneuston in the North Sea and in the Baltic. — Internat. Council for the Explor. of the Sea. C. M. 1969 L: 23, 1—14.

71. HERRING, P. J. (1965): Blue pigment of a surface-living oceanic copepod. — Nature 205, 103—104.

72. — (1969): Pigmentation and carotenoid metabolism of the marine isopod *Idotea metallica.* — J. mar. biol. Assoc. U. K. 49, 3, 766—779.

73. HUBBS, C. L. & KAMPA, E. M. (1946): The early stages (Egg, Prolarva and Juvenile) and the Classification of the California Flyingfish. — Copeia 4, 188—218.

74. HUNTER, J. R. & MITCHELL, C. T. (1967): Association of fishes with flotsam in the offshore waters of Central America. — Fish. Bull. U. S. Dep. Int. 66, 1, 13—29.

75. — — (1968): Field experiments on the attraction of pelagic fish to floating objects. — J. Cons. perm. int. Expl. Mer 31, 3, 427—434.

76. JERLOV, N. G. (1968): Optical Oceanography. — Elsevier Publ. Co., Amsterdam, London, New York.

77. KINZER, J. & HEMPEL, G. (1970): Probleme und Methoden der planktologischen Arbeiten auf den Atlantischen Kuppenfahrten von F. S. „Meteor", März—Juli 1967. — „Meteor"-Forschungsergebn. D 7, 3—22.

78. KOJIMA, S. (1961): On food contents of the dolphin. — Bull. Jap. Soc. sci. Fish. 27, 625—629.

79. KOVALEVSKAJA, N. V. (1964): Entwicklung der „zweiflügeligen" fliegenden Fische der Gattung *Exocoetus* (Exocoetidae, Pisces), (Russ.). — Trudy Inst. Okeanol. (Moskva) 73, 204—223.

80. KREYSZIG, G. (1965): Statistische Methoden und ihre Anwendungen. — Göttingen.

81. KRISTENSEN, J. (1964): Hypersaline bays as an environment of young fish. — Proc. Gulf Caribb. Fish. Inst. **16,** 139—142.

82. KÜNNE, C. (1933): Weitere Untersuchungen zum Vergleich der Fangfähigkeit verschiedener Modelle von vertikal fischenden Plankton-Netzen. — Cons. perm. int. Expl. Mer Rapp. et Proc.-Verb. 83, 1—19. p. 58

83. LAUSCHER, F. (1961): Sonnen- und Himmelsstrahlung im Meer und in Gewässern. — In: Handbuch der Geophysik, Hrsg. F. LINKE & F. MÖLLER 8, 723—768. — Borntraeger Berlin.

84. LEBOUR, M. V. (1917): The food of post-larval fish. — J. mar. biol. Assoc. U. K. 11, 4, 433—469.

85. — (1919—1922): Feeding habits of some young fish. — The food of post-larval fish No. II (1918). — The Food of Young Fish No. III (1919). — J. mar. biol. Assoc. U. K. 12, 9—21, 22—47, 261—324.

86. — (1933): The importance of larval Mollusca in the plankton. — J. Cons. perm. int. Expl. Mer **8,** 3, 335—343.

87. LEIM, A. H. & SCOTT, W. B. (1966): Fishes of the Atlantic coast of Canada. — Fish. Res. Board of Canada Bull. 155.

88. LÜLING, K. H. (1958): Zufallsbeobachtungen an *Tetraodon somphongsi* (KLAUSEWITZ) und *Gyrinocheilus aymonieri* (TIRANT). — Aquar. Terrar. Z. **11,** 11—15.

89. MARAK, R. R. (1960): Food habits of larval cod, haddock, and coalfish in the Gulf of Maine and Georges Bank area, J. Cons. perm. int. Expl. Mer 25, 2, 147—157.

90. MARINARO, J. & BERNARD, M. (1966): Contribution à l'étude des oefs et larves pélagiques de poissons méditerranéens. Note préliminaire sur l'influence léthale du rayonnement soleire sur les oefs. — Pelagos **6,** 49—55.

91. MARINARO, J. & HENRY, J. (1968): Sur un nouvel engin collecteur d'hyponeuston et son utilisation dans la baie d'Algier. — Pelagos **8,** 71—78.

92. MARSHALL, S. M. & ORR, A. P. (1955): The biology of a marine Copepod *Calanus finmarchicus* (Gunnerus). — London.

93. McLAREN, I. A. (1963): Effects of temperature on growth of zooplankton, and the adaptive value of vertical migration. — J. Fish. Res. Board of Canada. **20,** 685—727.

94. MIELCK, W. (1925): Heringslarven, Eier und Larven anderer Fische und Nahrung der Larven in der westlichen Nordsee im Oktober 1922. — Ber. Dt. wiss. Komm. Meeresforsch. N. F. **1,** 209—246.

95. MOHR, E. (1937): Revision der Centriscidae. — Dana-Rep. **13.**

96. MOORE, W. G. (1941): Studies on the feeding habits of fishes. — Ecology 22, 91—96.

97. MOROZOVSKAYA, O. (1966): Appartenance zoogéographique des Tintinnoidea à l'horizon pélagique superficiel de la Mer Noire. — 4me Conf. Zoogeogr., Odessa, C. R. (en russe) (nicht gesehen), 176—177.

98. MORRIS, R. W. (1955): Some considerations regarding the nutrition of marine fish larvae. — J. Cons. perm. int. Expl. Mer 20, 3, 255—265.

99. NAUMANN, E. (1917): Über das Neuston des Süßwassers. — Biol. Cbl. 37, 2, 98—106.

100. NOBRE, A. (1935): Vertebrados. — Fauna Marinha de Portugal I, Porto.

101. NORMAN, J. & FRASER, F. (1963): Riesenfische, Wale und Delphine. — Hamburg, Berlin (Übersetz.).

102. ODUM, E. P. (1967): Ökologie. — München, Basel, Wien.

103. OKADA, Y. & SUZUKI, K. (1951): A review on the *Macrorhamphosus* fishes of Japan. — Rep. Fac. Fish. Prefect. Univ. Mie **1**, 1, 7—11.

104. PARIN, N. V. (1967): Diurnal variations in the larval occurrence of some oceanic fishes near the ocean surface. — Oceanology **7**, 115—121.

105. PENNELL, W. (1967): Preliminary report on a study of neuston in the Gulf of St. Lawrence. — Rapp. Ann. Station Biol. Mar. Grande-Rivière, 55—60.

106. PFEIFFER, W. (1960): Über die Schreckreaktion bei Fischen und die Herkunft des Schreckstoffes. — Z. vergl. Physiol. **43**, 578—614.

107. PILLAY, T. V. (1953): A critique of the methods of study of food of fishes. — J. Zool. Soc. India **4**, 185—200.

108. RICHARDS, S. W. (1959): Pelagic fish eggs and larvae of Long Island Sound. — Bull. Bingham Oceanogr. Coll. **17**, 1, 95—124.

109. RUTTNER, F. (1962): Grundriß der Limnologie. — Berlin.

110. SAMEOTO, D. D. & JAROSZYNSKI, L. O. (1969): Otter surface sampler: a new neuston net. — J. Fish. Res. Board of Canada **26**, 8, 2240—2244.

111. SAVILOV, A. I. (1956): Pleustonbiozönose der *Velella lata* CHAMISSO und EISENHARDT, Siphonophoren, im Pazifik. — Dokl. Akad. Nauk. SSSR (Russ.) **110**, 3, 476—479.

112. — (1963): Pleustonsammelmethoden auf der E. S. Witjas (Russ.). — Okeanologija **3**, 523—526.

113. SCHIEMENZ, P. (1922): Über Nahrungsuntersuchungen bei Wassertieren, insbesondere Fischen. — Z. Fisch. NF **5**, 49—65.

114. SCHNAKENBECK, W. (1955): Pisces. — In: Handbuch der Zoologie Hrsg. J.-G. HELMCKE & H. v. LANGERKEN **6**, 1, 7. — Berlin.

115. SCHUTZ, F. (1956): Vergleichende Untersuchungen über die Schreckreaktion bei Fischen und deren Verbreitung. — Z. vergl. Physiol. **38**, 84—135.

116. SCHWOERBEL, J. (1966): Methoden der Hydrobiologie. — Stuttgart.

117. Sears Foundation for Marine Research, (1964): Fishes of the Western North Atlantic, **1**, 4. — New Haven.

118. SHOJIMA, Y. & UEKI, K. (1964): Studies on the larvae and juveniles of fishes accompanying floating algae II. — Bull. Japan. Soc. Sci. Fish. **30**, 3, 248—254.

119. SPECCHI, M. (1968): Observations préliminaires sur l'hyponeuston du golfe de Trieste. — Rapp. Comm. int. Mer Médit. **19**, 3, 491—494.

120. SUND, P. N. & RICHARDS, W. J. (1965): Results of trials with a neuston net in the Gulf of Guinea. — Ocean Sci. and Ocean Eng. 1965, Mar. Techn. Soc. Amer. Soc. Limn. **1**, 516—523.

121. TIMMERMANN, G. (1932): Biogeographische Untersuchungen über die Lebensgemeinschaft des treibenden Golfkrautes. — Z. Morphol. Ökol. Tiere **25**, 288—335.

122. TSIBAN, A. (1967): Dispositiv de prélèvement des échantillons microbiologiques dans le microhorizon supérieur de la mer noire (en russe). — Gidrobiol. Zhurn. **2**, 84—86.

123. TVEITE, S. & Danielsen, D. S. (1969): Funn Av Neustonorganismer I Norske Farvann. — Fiskets Gang **18**, 292—296.

124. UCHIDA, K. & SHOJIMA, Y. (1958): Studies on the larvae and juveniles of fishes accompanying floating algae I. — Bull. Japan. Soc. Sci. Fish. (Engl. Zusammenf.) **24**, 6, 411—415.

125. VALKANOV, A. (1968): Das Neuston. — Limnologica (Berlin) **6**, 2, 381—403.

126. VINOGRADOV, A. (1966): Biologie des Hyponeuston vom Nordosten des Schwarzen Meeres, Region der Insel Berezan. (Russ.). — Gidrobiol. Zhurn. 6.

127. — (1970) Some ecological-morphological adaptations of ichthyoneuston of the Black sea. (Russisch, engl. Zusammenf.) — Zool. Zhurn. 49, 9, 1366—1369.

128. WAHLERT, G. v. (1963): Die ökologische und evolutorische Bedeutung der Fischschwärme. — Veröff. Inst. f. Meeresforsch. Bremerhaven, Sonderbd., 197—213.

129. WICKSTEAD, J. H. (1965): An introduction to the study of tropical plankton. — Hutchinsons Tropic. Monogr., London.

130. WILLIAMS, P. M. (1967): Sea surface chemistry: organic carbon and organic and inorganic nitrogen and phosphorus in surface films and subsurface waters. — Deep-Sea Res. 14, 6, 791—800.

131. WINSOR, C. P. & CLARKE, G. L. (1940): A statistical study of variation in the catch of plankton nets. — J. Mar. Res. 3, 1, 1—34.

132. WOODHEAD, P. M. (1966): The behaviour of fish in relation to light. — Oceanogr. Mar. Biol. Rev. 4, 337—403.

133. YASUDA, F. & HIYAMA, Y. (1957): Mechanism of utilization of plankton by some fishes. — Rec. Oceanogr. Works in Japan, 3, 1, 85—91.

134. ZAITSEV, Y. P. (1959): On the methods of collecting pelagic eggs and fish larvae in the Regions of the Sea unexposed to considerable water freshening (Russ.). — Zool. Zhurn. 38, 9, 1426—1428. p. 59

135. — (1960): Die Neustonbiozönose im marinen pelagischen Leben (Ukrain.). — Naukovi Zapiski Odessa. 2, 1, 37—42.

136. — (1961): Pelagische Oberflächenbiozönose des Schwarzen Meeres (Russ.). — Zool. Zhurn. 40, 6, 818—825.

137. — (1962): Apparate und Technik zum Studium des Hyponeuston (Russ.). — Voprosy Ekol. 4, 107—110.

138. — (1964): Hyponeuston des Schwarzen Meeres und seine Bedeutung (Russ.) (nicht gelesen). — Autoref. diss. doct. biol. scient. Odessa, 3—22.

139. — (1967): Probleme der Meeres-Neustonologie (Russ.). — Gidrobiol. Zhurn. Kiew 3, 5, 58—69.

140. — (1968): La Neustonologie marine: Objet, Méthodes, Réalisations principales et Problèmes. — Pelagos, 8, 1—48.

141. ZELEZINSKAYA, L. (1966): Mortalité naturelle de certaines formes d'ichthyo- et de zooplankton en Mer Noire (en russe) (nicht gesehen). — Autoref. Diss. Cand. Sci. biol. Odessa, 3—20.

142. ZUSSER, S. G. (1956): Tagesperiodische Vertikalwanderung pelagischer planktotropher Fische (Russ.). — Rybn. Khoz. (Moskau) 5, 52—57.

1) Eggs and larvae of teleosts from West Africa; II. Vertical distribution.

4) Beginning and end of daily activity of free-living birds.

8) The tintinnids in the Mediterranean Sea.

11) The myctophids obtained at the Atlantic expedition "Petr Lebedev", 1961 -1964 (Russian text).

16) The absorption of solar radiation by the Sea, and its influence upon water temperature (Russian text).

17) Studies on the hydrology of the uppermost 1 m layer of water of the Black Sea. (Ukrainian text)

27) Atlantic plateau cruises 1967 with the research vessel "Meteor". Travel report and research results.

31) Eggs, larvae and juvenile stages of teleosts.

32) Herring larvae in the superficial layers of the Trondelag coast, April 1st, 1968.

37) The fauna of the oceanic superficial layer.

40) Distribution of pelagic fish-eggs and larvae in the Mediterranean Sea (Russian text).

42) The fishes of the Northmark.

43) Eggs and larvae of fishes. In: Northern plankton.

45) Ichthyological fauna of the North Atlantic.

46)

47)

51) Ocean biology.

53)

56) The food of oceanic animals. In: Handbook of the sea fishery of North Europe.

59) Distribution and food of ichthyoneuston in the subtropical NE-Atlantic.

60) Chalimus stages of Lepeophtheirus on juvenile Onos cimbrius and Onos mustelus.

61) Diurnal migration and vertical microdistribution of neustonic cephalopods west of Madeira.

63) Dependency of a neuston fish upon the superficial layer of the sea — behavior of juvenile Liza aurata in the observation pool and in its habitat.

64) Behavior of neuston in the observation pool.

65) Distribution of herring larvae and plankton on May 28, 1969 in the Schlei river (Schleswig-Holstein, Germany): volume of deposits.

66) Diurnal migration of a mictophyd (pisces) and of two neustonic mollusks that serve as its food.

70) Ichthyoneuston in the North Sea and in the Baltic Sea.

77) Problems and methods of planktological work during the Atlantic plateau cruises of the research vessel F.S. "Meteor", March-July 1967.

79) Development of the "double-winged" flying fish of the species Exocoetus (exocoetidae, pisces) (Russian text).

80) Statistical methods and their applications.

82) Additional investigations for comparison of the performance of diverse vertical fishing plankton nets.

83) Solar and celestial radiation in the sea and in inland waters. In: Handbook of geophysics.

88) Chance observations on Tetraodon somphongsi (KLAUSEWITZ) and Gyrinocheilus aymonieri (TIRANT).

91)

94) Herring larvae, eggs, and larvae of other fish, as well as food of larvae in the western North Sea in October 1922.

95) Examination of the centriscidae.

97)

99) On the neuston in fresh waters.

100) Vertebrates.

101) Giant fishes, wales, and dolphins.

102) Ecology.

106) On the fright reaction in fish, and the origin of the "fright substance".

109) Basic outline of limnology.

111) Pleuston biocoenosis of Velella lata CHAMISSO and EISENHARDT, siphonophores, in the Pacific Ocean. (Russian text)

112) Methods for the collection of neuston used aboard the E.S. Witjas (Russian text).

113) On the examination of food in aquatic animals, especially in fish.

114) Pisces. In: Handbook of zoology.

115) Comparative investigations on the fright reaction in fish, and its spreading.

116) Methods of hydrobiology.

119) Preliminary observations on the hyponeuston in the Gulf of Trieste.

121) Biographical studies on the conjugal existence of drifting gulfweed.

122)

123) Locating neuston organisms in Norwegian waters.

125) The neuston.

126) Biology of hyponeuston in the north-east of the Black Sea, region of the island of Berezan (Russian text).

128) The ecological and evolutionary significance of fish schools.

135) The neuston biocoenosis in pelagic marine life (Ukrainian text).

136) Pelagic surface biocoenosis in the Black Sea (Russian text).

137) Apparatus and techniques for the study of hyponeuston (Russian text).

138) Hyponeuston in the Black Sea and its importance (Russian text).

139) Problems of marine neustonology (Russian text).

140)

141)

142) Diurnal vertical migration of pelagic planktotrophic fish (Russian text).

Translator's note: For appendix (original p. 60) please see next page.

Appendix

Station log 1968

Day	Month	No.	North°	Position North'	West°	West'	Sampling time & speed Start	Terminated	Knots
19	4	N 1	47	20	06	16	10^{10}	10^{40}	5—6
19	4	N 2	46	35	06	55	22^{00}	22^{30}	5—6
20	4	N 3	45	13	07	51	10^{00}	10^{30}	5—6
20	4	N 4	43	33	09	08	22^{00}	22^{30}	5—6
21	4	N 5	41	44	10	00	10^{00}	10^{30}	5—6
22	4	N 6	39	48	10	41	10^{00}	10^{30}	5—6
23	4	N 7	33	45	12	50	10^{00}	10^{30}	5—6
23	4	N 8	31	44	13	33	22^{00}	22^{30}	5—6
24	4	N 9	29	35	14	18	10^{00}	10^{30}	5—6
24	4	N 10	27	32	14	46	22^{00}	22^{30}	5—6
25	4	N 11	26	07	15	02	05^{35}	06^{05}	5—6
02	5	N 12	20	59	17	30	21^{40}	22^{10}	5—6
02	5	N 13	20	54	17	25	22^{35}	23^{05}	5—6
02	5	N 14	20	49	17	23	23^{10}	23^{40}	5—6
03	5	N 15	20	47	17	12	10^{10}	10^{40}	6
03	5	N 16	20	40	17	29	13^{40}	14^{10}	6
03	5	N 17	20	41	17	45	18^{15}	18^{45}	5—6
04	5	N 18	20	40	18	01	05^{10}	05^{40}	5—6
04	5	N 19	20	40	18	34	10^{25}	10^{55}	5—6
04	5	N 20	20	40	18	46	16^{05}	16^{35}	5—6
07	5	N 21	20	20	17	11	13^{00}	13^{40}	4
09	5	N 22	20	20	19	22	13^{02}	13^{45}	3—4
09	5	N 23	20	24	18	40	18^{35}	19^{10}	5
13	5	N 24	20	22	17	29	10^{35}	11^{35}	3
13	5	N 25	20	16	17	30	11^{40}	12^{35}	3
13	5	N 26	19	42	18	43	23^{25}	00^{05}	5—6
14	5	N 27	19	40	18	52	15^{05}	15^{35}	5
15	5	N 28	19	40	18	03	01^{15}	01^{45}	6
15	5	N 29	19	40	17	42	11^{23}	11^{55}	5
15	5	N 30	19	40	17	31	18^{03}	18^{38}	5
16	5	N 31	19	38	17	08	05^{12}	05^{46}	5
17	5	N 32	19	53	17	32	08^{50}	09^{20}	6
19	5	N 33	19	22	16	47	15^{25}	15^{55}	6
19	5	N 34	19	19	17	02	17^{55}	18^{30}	4
19	5	N 35	19	18	17	11	22^{10}	22^{35}	4
20	5	N 36	19	16	17	21	02^{18}	02^{48}	6
20	5	N 37	19	12	17	44	07^{40}	08^{25}	4—5
27	5	N 38	21	06	17	15	17^{30}	18^{05}	5
28	5	N 39	21	58	18	55	16^{05}	16^{35}	6
29	5	N 40	22	03	18	24	18^{58}	19^{28}	5—6
29	5	N 41	22	03	18	24	19^{33}	20^{00}	5—6
30	5	N 42	22	03	19	24	00^{45}	01^{15}	5—6
30	5	N 43	22	06	18	01	03^{00}	03^{30}	6
30	5	N 44	22	01	17	48	08^{25}	08^{55}	5—6
30	5	N 45	22	01	17	48	13^{20}	13^{50}	5—6
30	5	N 46	22	00	17	16	20^{25}	20^{55}	6
30	5	N 47	22	00	17	13	22^{27}	22^{57}	5—6
31	5	N 48	21	47	17	19	07^{50}	08^{20}	6
31	5	N 49	21	30	17	11	10^{40}	11^{10}	6
31	5	N 50	21	30	17	17	11^{20}	11^{50}	6
31	5	N 51	21	30	17	17	11^{55}	12^{25}	6
31	5	N 52	21	30	17	24	12^{35}	13^{05}	6
31	5	N 53	19	32	21	28	23^{34}	24^{04}	6
01	6	N 54	19	15	21	26	15^{55}	16^{25}	5—6
02	6	N 55	18	47	21	23	04^{08}	04^{38}	5—6
02	6	N 56	18	32	21	22	06^{15}	06^{45}	5
02	6	N 57	18	18	21	27	12^{30}	13^{00}	5
02	6	N 58	18	11	21	26	22^{48}	23^{18}	5—6
03	6	N 59	21	32	17	58	05^{00}	05^{30}	5—6
03	6	N 60	21	38	17	36	10^{40}	11^{10}	5—6
03	6	N 61	21	33	17	37	13^{35}	14^{05}	5—6
03	6	N 62	21	31	17	20	20^{45}	21^{15}	5—6