

Feeding Ecology and Stranding Mechanisms in Two Lanternfishes, *Hygophum benoiti* and *Myctophum punctatum*

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ABSTRACT: The feeding ecology of 2 vertically migrating midwater fishes – *Hygophum benoiti* and *Myctophum punctatum* – found stranded along the shores of the Straits of Messina was studied in order to reconstruct the ecological mechanisms involved in their stranding processes. Diet analyses revealed that both fishes fed mostly on copepods and euphausiids but also on a variety of other food items. Ontogenetic changes in the diet indicated that size selection determined prey choice in all stages in the life cycle of *H. benoiti*. *M. punctatum*, on the other hand, became opportunistic with age, adding new components to the diet without excluding prey items eaten by smaller individuals. At the species level, prey choice involved selective feeding on more visible prey items such as bioluminescent copepods. The prey population primarily included surface and migrating sub-surface species. Knowledge of prey vertical distribution patterns in the Mediterranean Sea suggests active feeding by both predators in surface waters at night. The absence of deep water non-migrating elements in the diet implies that the current hypothesis of passive transport of species due to surfacing deep water masses in the Straits may not hold true for all stranded organisms. Alternative stranding mechanisms involving active trophic migrations are proposed for midwater species known to undergo strong diel vertical movements.

INTRODUCTION

A most peculiar biological feature of the Straits of Messina, between Sicily and the Italian mainland, is the shore stranding of deep-water marine organisms. In the past this phenomenon attracted much attention from ecologists, yet to date little information is available on the physical and biological mechanisms involved in these strandings. One of the few detailed papers on this argument (Mazzarelli, 1909) consists of a list of species, including their time of stranding, over a period of 2 yr. Only recently has this list been incremented to include midwater fishes (Genovese et al., 1971) and pelagic and benthic crustaceans (Guglielmo et al., 1973).

The main cause in the stranding of midwater organisms is considered to be the complex hydrological regime (Vercelli, 1925; Defant, 1961), where surfacing deep-water masses in the Straits are thought literally to 'drag many deep-water organisms from their normal habitat' (Marshall, 1954). Subsequently, opposing tidal currents and favorable wind conditions, in particular

SE Sirocco winds, result in strandings along the coast. Little importance was credited to active migrations by midwater organisms to surface waters, although Mazzarelli (1909) hypothesized that passive transport to the surface may be facilitated by vertical migrations related to reproductive cycles, and Berdar et al. (1979) suggested that diel migrations may play an important role in this phenomenon.

To test the passive transport hypothesis we have undertaken a detailed study of the feeding ecology of the 2 most abundant midwater fishes to be washed ashore in this area, *Hygophum benoiti* (Cocco) and *Myctophum punctatum* Rafinesque. Both these myctophids are ranking midwater Mediterranean species, having day-depth distributions from 100 to 1000 m and maximum concentrations at 700–1000 m. They undergo marked diel vertical migrations reaching the surface layers at night (Goodyear et al., 1972). If in the Straits of Messina these 2 species feed at the surface, and if such trophic migrations are facilitated by upwelling waters, one would expect to find a mixed population in their stomach which includes deep-

water, non-migrating elements. A prey population consisting exclusively of typical surface-water species would disprove the passive transport hypothesis and encourage alternative explanations as to what mechanisms are involved in stranding processes.

MATERIAL AND METHODS

The specimens were collected by the Hydrobiology Department of the University of Messina. They included 145 individuals of *Hygophum benoiti* and 110 of *Myctophum punctatum*, sampled along the shores of the Straits of Messina near Faro, Ganzirri and S. Francesco (Fig. 1.). Beached material was collected early in the morning following strong onshore winds, in par-

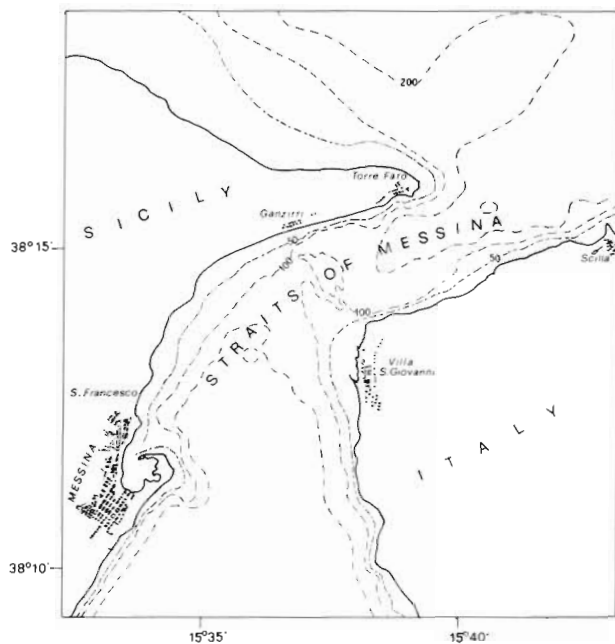


Fig. 1. Straits of Messina showing sampling sites

ticular SE (Sirocco) winds. Freshly stranded individuals were undamaged and some still alive. All *H. benoiti* were collected from March to June and August to December 1972; *M. punctatum* were collected from March to June and August to January 1972 to 1978. All specimens were measured to the nearest millimeter standard length (SL), separated according to sex; when possible, stomach contents were identified to species level. Size of individual prey was determined from intact specimens sampled in the Straits and adjacent areas. Biomass values were then calculated by assigning an average wet weight value to each prey item according to the method of Shmeleva (1965).

A multivariate analysis technique known as 'RQ' analysis (Hathaway, 1971) or Reciprocal Averaging

(Hill, 1973) was performed on all data. This technique, as well as others such as Factor Analysis of Correspondences (Benzecri, 1980), was particularly useful in the 'ordination of ecological systems' (Orloci, 1975), producing models in which the R^n space of n observations and the R^m space of m variables were isomorphic thus giving observations and variable points which could be projected on the same factorial space. Proximities between variable and observation points reflected reciprocal relationships. The significance of the models obtained with this technique was tested by a method proposed by Frontier (1974): a factor was considered significant when it explained more variance than it predicted by MacArthur's (1960) 'broken stick model'. Diversity of species and/or taxa (H') was calculated by means of the Shannon-Weaver formula, along with theoretical maxima-minima and redundancy (Patten, 1962). All calculations were performed on an Olivetti P 6060 minicomputer and are based on original programs and those adapted from Orloci (1975).

RESULTS

Hygophum benoiti (Cocco, 1838)

Hygophum benoiti was found stranded throughout the year in the Straits of Messina. Table 1 shows the stranding frequency recorded during the course of the present investigation. The largest number of stranded specimens occurred in autumn and winter. Males stranded more frequently than females ($X^2 = 15.5588$; 135 d.o.f.; $p < .005$) in all months except October. Nine of the 145 individuals could not be identified to sex.

Most of the specimens examined were adults (> 40 mm) or subadults (20 to 40 mm). Body length ranged from 21 to 60 mm with an annual mean of 44.11 mm (SD = 8.964). No significant difference was found between the mean annual length of males and females. The length-frequency distribution throughout the year is shown in Fig. 2. Mean body length steadily increased from early spring to late summer and decreased from October onwards. A minimum occurred in December when the population seemed to be entirely renewed. Reproduction probably reached a peak between April and September with early recruits appearing in October-November (Fig. 2a).

Of the 145 specimens sampled, 131 had full or partially full stomachs while the remaining 14 were empty. The complete faunistic spectrum for all seasons included 99 taxa (77 identified to the species level) belonging to 7 major groups as listed in Table 2. Copepods and euphausiids (mainly juveniles) were dominant food items, representing 88.2% and 9.0%

Table 1. *Hygophum benoiti* and *Myctophum punctatum*. Stranding frequency

	Jan	Mar	Apr	May	Jun	Aug	Sep	Oct	Nov	Dec	Total
<i>H. benoiti</i>											
♂♂	–	29	6	8	3	2	9	12	2	20	91
♀♀	–	15	0	4	0	0	0	18	1	8	45
Total	–	44	6	12	3	2	9	30	3	28	136
<i>M. punctatum</i>											
♂♂	3	6	2	1	3	2	6	0	7	8	38
♀♀	1	10	1	1	2	4	0	40	5	2	66
Total	4	16	3	2	5	6	6	40	12	10	104

Table 2. *Hygophum benoiti* (H) and *Myctophum punctatum* (M). Principal prey taxa in the diet

Prey taxa	No. species		Prey items		% No.		% wet weight	
	H	M	H	M	H	M	H	M
Copepods	57	70	3,089	5,711	88.2	82.5	27.3	40.3
Euphausiids	4	8	318	302	9.0	4.3	71.3	54.0
Amphipods	7	25	23	128	0.7	1.9	0.6	2.5
Mysiids	4	4	11	9	0.3	0.1	0.2	0.1
Ostracods	2	2	13	15	0.4	0.2	0.1	0.1
Chaetognaths	–	–	24	172	0.7	2.5	0.5	2.7
Appendicularians	–	–	1	400	–	5.8	–	0.3
Others	3	11	25	190	0.7	2.7	–	–

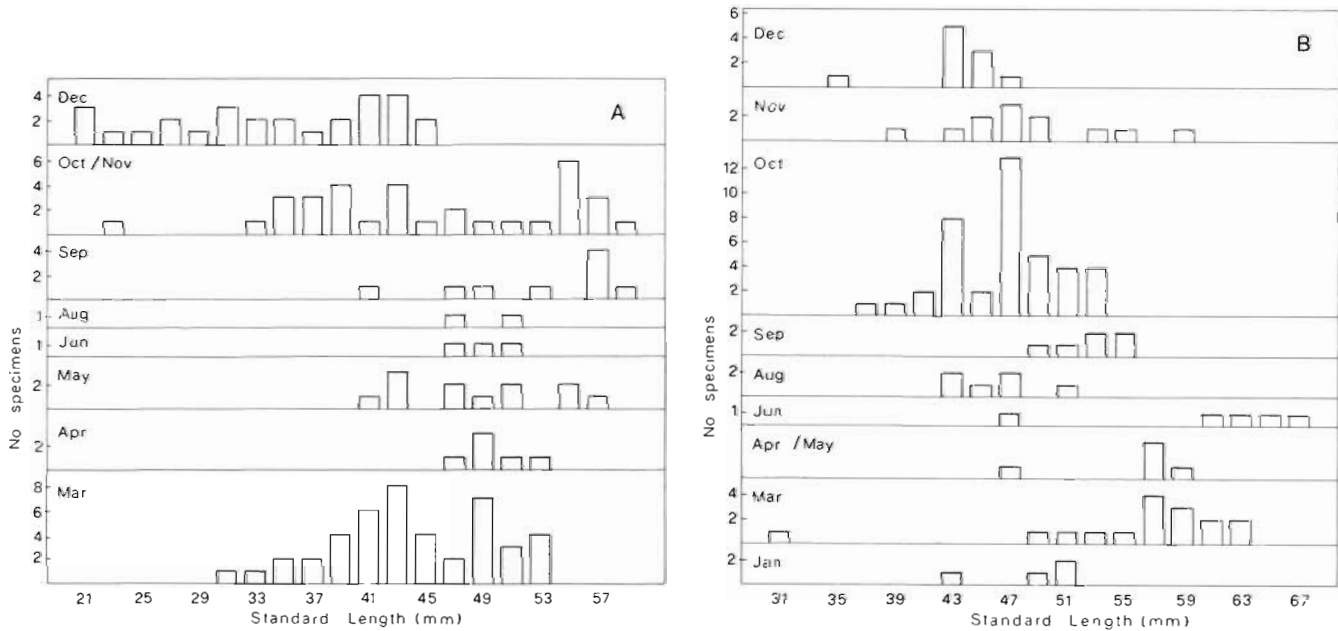


Fig. 2. *Hygophum benoiti* (A) and *Myctophum punctatum* (B). Annual size distribution (SL) of stranded specimens

respectively of the total prey population as individuals and 27.3% and 71.3% respectively as biomass. The remaining taxonomic groups represented an insignificant fraction of the overall diet.

A species list of the stomach contents was compiled by pooling number of prey items for all seasons (Table 3). The list included 57 copepod, 4 euphausiid, 8 amphipod, 2 ostracod, 4 mysiid, 3 pteropod and 1 thaliacean species. Included were also several taxonomic groups such as chaetognaths, appendicularians, decapod and fish larvae which were not identified to the species level. The most dominant copepods occurring annually were species of the genus *Pleuromamma* (mainly *P. abdominalis* and *P. gracilis*), *Nannocalanus minor*, *Oncaea mediterranea*, *Euchaeta marina*, *Temora stylifera*, *Lucicutia flavicornis*, *Paracandacia simplex*, *Candacia aethiopica*, *Neocalanus gracilis* and *Euchaeta* sp. which together represented 91.6% of the total number of identified copepods. Among the euphausiids, *Euphausia krohnii* and *Meganyctiphanes norvegica* were the 2 main species eaten.

On a seasonal basis (Table 4), *Hygophum benoiti* fed mostly on copepods (*Pleuromamma* sp., *P. abdominalis*, *P. gracilis*, *Oncaea mediterranea* and *Nannocalanus minor*) and some euphausiids in winter and spring, but fed almost exclusively on copepods in autumn. During summer, euphausiids were dominant food items, particularly *Euphausia krohnii*. A synoptic picture regarding seasonal trends in the entire population was also given by an RQ analysis using the 7 major taxonomic groups (Table 2) as variables and 131 specimens as observations. The analysis was performed both on numerical abundances and biomass values. In the case of abundance values little information was obtained since the same weight was given to taxa having greatly different biomasses, i.e. an appendicularian or a copepod ranked in exactly the same way as a much larger euphausiid. The results of RQ analysis using biomass values is shown in Fig. 3a. The first two factors both significant explained 55.99% and 21.49%, respectively, of the total variance. The correlation between prey taxa and fish specimen scores was 0.736 for F1 and 0.456 for F2. The first axis opposed copepods with euphausiids. Amphipods, chaetognaths, appendicularians, mysids and ostracods were located near the mid-point (O correlation). In the space of F2, mysids were opposed to all other groups. Fish specimen-points were ordered linearly between the 2 extremes. The observations concentrated near the copepod pole represented *H. benoiti* specimens collected in all 4 seasons but, above all, those collected in winter and autumn. Summer observations were concentrated near the euphausiid pole. Several spring and some autumn observations were scattered all along F1

but in particular in the central portion of the diagram. Individuals of *H. benoiti*, having respectively small sizes (copepod pole) and large sizes (euphausiid pole) were grouped at the opposite poles of the diagram. This was demonstrated by the highly significant correlation value ($r = .539$) between F1 and fish size. Prey biomass increased from the diagram's mid-point towards the opposite poles whereas diversity of prey items decreased towards both poles.

Myctophum punctatum Rafinesque, 1810

Myctophum punctatum in the Straits of Messina was found stranded throughout the year. The stranding frequency recorded during the present investigation appears in Table 1. The annual sex ratio was in favor of females ($X^2 = 7.538$; 103 d.o.f.; $p < .005$) due to the high number of stranded females in October. Two of the 106 specimens could not be identified to sex.

Most of the specimens were adults (> 45 mm) or subadults (20 to 45 mm). Body length ranged from 22 to 68 mm with an annual mean of 49.69 mm (SD = 7.119). No significant difference was found between the mean annual length of males and females. The length-frequency distribution throughout the year is given in Fig. 2B. Mean body length increased from March to September and steadily decreased thereafter reaching a minimum in December. Smaller size classes appeared mostly from October onwards. These results suggest that reproduction reached a peak during spring and early summer.

Of the 106 specimens sampled, 101 had full or partially full stomachs and 5 were empty. The complete faunistic spectrum for all seasons included 152 taxa (125 identified to the species level) belonging to 7 major groups as listed in Table 2. Copepods and euphausiids (mainly juveniles) were the dominant food items comprising 82.5% and 4.3% respectively of the total prey population in terms of individuals and 40.3% and 54.0% respectively in terms of biomass. Of the remaining species, appendicularians and chaetognaths contributed respectively 5.7% and 2.5% of the total number of prey individuals.

A species list of the stomach contents for *Myctophum punctatum* is given in Table 5. The list included 71 copepod, 8 euphausiid, 28 amphipod, 3 ostracod, 4 mysiid, 5 pteropod, 3 polychaete, 1 thaliacean, 1 fish and 1 isopod species. The list also included other taxonomic groups such as heteropods, chaetognaths, appendicularians, nematodes, hydromedusae, decapod and cirripede larvae which were not identified to the species level. Several of the species recorded were benthic or benthoplanktonic. In particular,

Table 3. *Hygophum benoiti*. List of prey species found in 145 specimens

Food category	Total	Food category	Total	Food category	Total
Copepods		Ostracods			
<i>Calanus helgolandicus</i>	2	<i>Paracandacia bispinosa</i>	1	<i>Conchoecia haddoni</i>	3
<i>C. tenuicornis</i>	1	<i>P. simplex</i>	40	<i>C. obtusata</i>	3
<i>Nannocalanus minor</i>	198	<i>Candacia</i> spp.	11	<i>Conchoecia</i> spp.	3
<i>Neocalanus gracilis</i>	32	<i>Oncaea conifera</i>	5	Unidentified	4
<i>Calanus</i> spp.	18	<i>O. media</i>	10	Mysiids	
<i>Eucalanus monachus</i>	3	<i>O. mediterranea</i>	125	<i>Lophogaster typicus</i>	3
<i>Paracalanus parvus</i>	1	<i>O. venusta</i>	1	<i>Gastrosaccus lobatus</i>	1
<i>Calocalanus contractus</i>	1	<i>Oncaea</i> spp.	3	<i>G. sanctus</i>	1
<i>C. pavo</i>	1	<i>Lubbockia squillimana</i>	2	<i>Gastrosaccus</i> sp.	1
<i>Clausocalanus arcuicornis</i>	17	<i>Sapphirina auronitens</i>	1	<i>Anchialina agilis</i>	2
<i>C. jobei</i>	1	<i>S. gemma</i>	1	Unidentified	3
<i>C. lividus</i>	8	<i>Copilia mediterranea</i>	1	Pteropods	
<i>C. mastigophorus</i>	4	<i>C. vitrea</i>	1	<i>Limacina inflata</i>	1
<i>C. parapergens</i>	11	<i>Corycaeus clausi</i>	9	<i>L. trochiformis</i>	4
<i>C. pergens</i>	1	<i>C. flaccus</i>	3	<i>Limacina</i> sp.	1
<i>Clausocalanus</i> spp.	11	<i>C. furcifer</i>	1	<i>Creseis virgula</i>	3
<i>Euaetideus giesbrechti</i>	3	<i>C. giesbrechti</i>	1	<i>Creseis</i> sp.	1
<i>Chiridius poppei</i>	1	<i>C. rostrata</i>	1	Unidentified	6
<i>Euchirella messinensis</i>	12	<i>C. typicus</i>	3	Polychaetes	
<i>Euchaeta acuta</i>	6	Unidentified	422	Unidentified fragments	1
<i>E. hebes</i>	2	Euphausiids			
<i>E. marina</i>	113	<i>Euphausia krohnii</i>	129	Chaetognaths	
<i>Euchaeta</i> spp.	38	<i>Euphausia</i> spp.	6	<i>Sagitta</i> sp.	24
<i>Scolecithrix bradyi</i>	1	<i>Meganyctiphanes norvegica</i>	113	Thaliaceans	
<i>S. danae</i>	1	<i>Nematoscelis megalops</i>	7	<i>Thalia democratica</i>	1
<i>Scolecithricella dentata</i>	3	<i>Nematoscelis</i> sp.	1	Appendicularians	
<i>Centropages typicus</i>	3	<i>Stylocheiron longicorne</i>	1	<i>Oikopleura</i> sp.	1
<i>C. violaceus</i>	3	<i>Stylocheiron</i> sp.	1	Fishes	
<i>Temora stylifera</i>	87	Unidentified	41	<i>Cyclotone</i> sp.	1
<i>Pleuromamma abdominalis</i>	424	Larvae	19	Others	
<i>P. borealis</i>	2	Hyperiid amphipods			
<i>P. gracilis</i>	178	<i>Phronima atlantica</i>	1	Decapod larvae	5
<i>P. piseki</i>	8	<i>Phronimella elongata</i>	2	Cirripede larvae	1
<i>P. robusta</i>	1	<i>Lestrigonus schizogeneios</i>	4		
<i>Pleuromamma</i> spp.	1128	<i>Lestrigonus</i> spp.	4		
<i>Lucicutia flavicornis</i>	45	<i>Phrosina semilunata</i>	3		
<i>L. gemina</i>	10	<i>Primno macropa</i>	1		
<i>Heterorhabdus abyssalis</i>	1	<i>Tetrathyrus forcipatus</i>	1		
<i>H. papilliger</i>	4	<i>Brachyscelus cruscolum</i>	3		
<i>Candacia aethiopica</i>	34	Gammariid amphipods			
<i>C. armata</i>	9	Unidentified	4		
<i>C. bipinnata</i>	3				
<i>C. giesbrechti</i>	2				
<i>C. longimana</i>	11				

amphipods such as *Gammarus olivii*, *Dexamine* spp., *Apherusa mediterranea*; the mysiid *Siriella jaltensis*; isopods of the genus *Euridice*; ostracods of the genus *Philomedes*; and nematodes are strictly benthic or make only brief appearances in the plankton, especially at night (e.g. *Euridice* and *Dexamine*).

The most dominant copepods occurring annually were *Nannocalanus minor*, *Temora stylifera*, *Pleuromamma* sp., *P. abdominalis*, *P. gracilis*, *Euchaeta marina*, *Euchirella messinensis*, *Paracandacia simplex*, *Neocalanus gracilis*, *Clausocalanus*

lividus, *C. parapergens*, *Lucicutia flavicornis* which together represented 88.0% of the total number of identified copepods. Among the euphausiids, *Meganyctiphanes norvegica* and *Euphausia krohnii* were the 2 main species eaten.

On a seasonal basis (Table 6), *Myctophum punctatum* fed primarily on copepods, showing no definite dominance of food items, except for summer when *Nannocalanus minor*, *Temora stylifera*, *Euchaeta marina* and *Pleuromamma* sp. were the dominant prey. Euphausiids were important in spring (namely

Table 4. *Hygophum benoiti*. Seasonal occurrence of more abundant (>1%) prey species in the diet (mean no. stomach⁻¹)

Prey	Winter	Spring	Summer	Autumn
Copepods				
<i>Pleuromamma</i> sp.	10.39	22.23	0.36	2.38
<i>Pleuromamma abdominalis</i>	3.02	5.59	2.73	2.00
<i>Nannocalanus minor</i>	1.93	0.59	0.18	1.42
<i>Pleuromamma gracilis</i>	0.85	1.91	0.18	1.44
<i>Oncaea mediterranea</i>	2.59	0.14	–	0.05
<i>Euchaeta marina</i>	0.28	0.41	–	1.38
<i>Temora stylifera</i>	0.09	0.23	0.36	1.12
<i>Lucicutia flavicornis</i>	0.20	–	–	0.55
<i>Paracandacia simplex</i>	0.17	0.09	0.09	0.44
<i>Euchaeta</i> sp.	0.22	0.45	0.36	0.21
<i>Neocalanus gracilis</i>	0.24	0.18	–	0.26
<i>Candacia aethiopica</i>	0.02	–	0.09	0.45
Unidentified	21.67	33.18	5.00	13.38
Euphausiids				
<i>Meganyctiphanes norvegica</i>	2.22	0.27	0.45	–
<i>Euphausia krohnii</i>	0.20	1.27	5.00	0.56
Unidentified	2.52	1.55	5.73	0.68

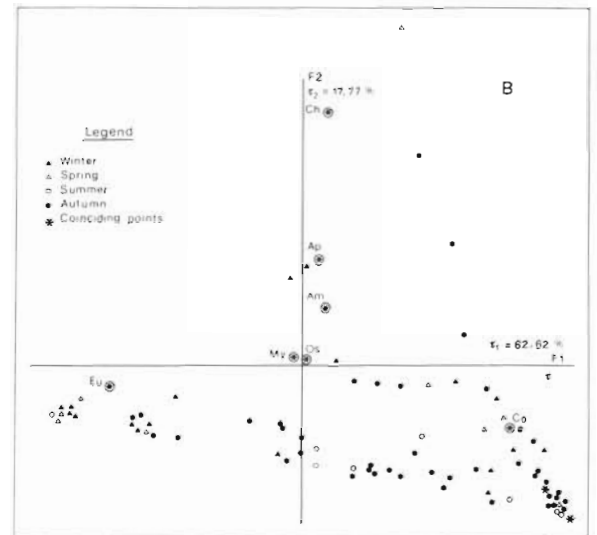
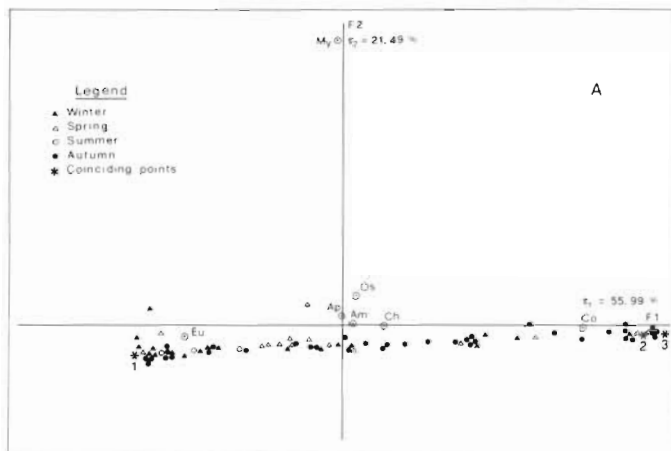


Fig. 3. RQ Analysis: Ordination model in the plane of the first two factors (F1 and F2), showing seasonal trends in diet composition of (A) *Hygophum benoiti* and (B) *Myctophum punctatum* and biomass values of various taxonomic groups (τ = percentage of variance). Prey taxa: Co copepods, Eu euphausiids, Ap appendicularians, Am amphipods, Os ostracods, Ch chaetognaths, My mysids. Coinciding points for *H. benoiti* include: Point 1 • = 7 winter, 7 summer and 5 autumn observations; Point 2 • = 3 winter and 2 autumn observations; Point 3 • = 11 winter, 7 spring and 17 autumn observations, and for *M. punctatum*: 3 winter, 1 spring, 4 summer and 10 autumn observations

Euphausia krohnii) and especially in winter (*Meganyctiphanes norvegica*). Benthoplankters occurred only sporadically and did not show any apparent seasonal trends in the diet. Seasonal trends in the entire population were also analyzed by the RQ method using the 7 major taxonomic groups as variables and the 101 specimens as observations. The analysis was performed on both numerical abundances

and biomass values. Results obtained from abundance values gave little information as compared to those obtained from biomass values (for the same reason as for *Hygophum benoiti*). Therefore only these latter results are discussed. Fig. 3B shows the ordination model in the plane of the first two factors that explained respectively 62.62% and 17.77% of the total variance, both being significant. The correlation of the

Table 5. *Myctophum punctatum*. List of prey species found in 106 specimens

Food category	Total	Food category	Total	Food category	Total
Copepods				Ostracods	
<i>Calanus helgolandicus</i>	14	<i>O. venusta</i>	2	<i>Conchoecia haddoni</i>	2
<i>C. tenuicornis</i>	42	<i>Pachos punctatum</i>	1	<i>Conchoecia</i> sp.	1
<i>Nannocalanus minor</i>	1144	<i>Sapphirina auronitens</i>	3	<i>Philomedes globosus</i>	1
<i>Neocalanus gracilis</i>	93	<i>S. nigromaculata</i>	1	<i>Philomedes</i> sp.	1
<i>Calanus</i> spp.	9	<i>S. opalina</i>	3	<i>Cylindroleberis</i> spp.	8
<i>Eucalanus attenuatus</i>	1	<i>Copilia vitrea</i>	2	Unidentified	2
<i>E. elongatus</i>	5	<i>Corycaeus clausi</i>	38	Mysiids	
<i>E. monachus</i>	4	<i>C. flaccus</i>	26	<i>Siriella clausi</i>	2
<i>Paracalanus nanus</i>	2	<i>C. furcifer</i>	4	<i>S. jaltensis</i>	1
<i>Calocalanus pavo</i>	25	<i>C. ovalis</i>	2	<i>S. norvegica</i>	2
<i>Mecynocera clausi</i>	1	<i>C. rostrata</i>	11	<i>Siriella</i> sp.	1
<i>Clausocalanus arcuicornis</i>	38	<i>C. typicus</i>	15	<i>Anchialina agilis</i>	3
<i>C. furcatus</i>	4	<i>Monstrilla</i> sp.	1	Pteropods	
<i>C. jobei</i>	7	Unidentified	990	<i>Limacina inflata</i>	6
<i>C. lividus</i>	61	Euphausiids		<i>Limacina</i> spp.	5
<i>C. mastigophorus</i>	8	<i>Euphausia brevis</i>	2	<i>Creseis acicula</i>	17
<i>C. parapergens</i>	57	<i>E. hemigibba</i>	3	<i>C. virgula</i>	1
<i>C. paululus</i>	1	<i>E. krohnii</i>	47	<i>Creseis</i> spp.	16
<i>C. pergens</i>	8	<i>Meganyctiphanes norvegica</i>	180	<i>Hyalocylis striata</i>	1
<i>Clausocalanus</i> spp.	5	<i>Nematoscelis atlantica</i>	1	<i>Cavolinia inflexa</i>	1
<i>Ctenocalanus vanus</i>	1	<i>N. megalops</i>	20	<i>Cavolinia</i> sp.	1
<i>Aetideus armatus</i>	2	<i>Stylocheiron longicorne</i>	5	Unidentified	3
<i>Euaetideus giesbrechti</i>	13	<i>Thysanopoda eequalis</i>	1	Heteropods	
<i>Chiridius poppei</i>	1	Unidentified	3	Unidentified	51
<i>Euchirella messinensis</i>	238	Larvae	40	Polychaetes	
<i>Euchaeta acuta</i>	13	Amphipods		<i>Vanadis cristallina</i>	1
<i>E. marina</i>	242	Hyperiid		<i>Vanadis</i> sp.	2
<i>E. spinosa</i>	6	<i>Scina crassicornis</i>	1	<i>Callizona angelini</i>	4
<i>Euchaeta</i> spp.	25	<i>Vibilia armata</i>	4	<i>C. setosa</i>	1
<i>Scolecithricella abyssalis</i>	1	<i>V. cultripes</i>	2	Unidentified fragments	151
<i>S. dentata</i>	1	<i>Vibilia</i> sp.	1	Chaetognaths	
<i>Centropages kröyeri</i>	1	<i>Phronima colletti</i>	2	<i>Sagitta</i> spp.	172
<i>C. typicus</i>	24	<i>P. sedentaria</i>	3	Thaliaceans	
<i>C. violaceus</i>	19	<i>P. stebbingi</i>	3	<i>Thalia democratica</i>	6
<i>Temora stylifera</i>	890	<i>Phronima</i> sp.	1	Unidentified fragments	258
<i>Pleuromamma abdominalis</i>	400	<i>Lestrigonus schizogeneios</i>	15	Appendicularians	
<i>P. borealis</i>	1	<i>L. latissimus</i>	4	<i>Oikopleura</i> spp.	400
<i>P. gracilis</i>	282	<i>Hyperietta luzoni</i>	1	Fishes	
<i>P. piseki</i>	1	<i>H. stephenseni</i>	1	<i>Cyclotone braueri</i>	2
<i>P. robusta</i>	15	<i>Phronimopsis spinifera</i>	26	<i>Cyclotone</i> sp.	2
<i>Pleuromamma</i> spp.	483	<i>Phrosina semilunata</i>	4	Larvae	14
<i>Lucicutia clausi</i>	6	<i>Lycaea</i> sp.	1	Eggs	2
<i>L. flavicornis</i>	65	<i>Parascelus typhoides</i>	14	Isopods	
<i>L. gemina</i>	14	<i>Brachyscelus crusculum</i>	2	<i>Eurydice inermis</i>	3
<i>Heterorhabdus abyssalis</i>	2	<i>Simorhynchotus antennarius</i>	1	<i>Eurydice</i> sp.	2
<i>H. papilliger</i>	2	<i>Calamorrhynchus pellucidus</i>	1	Others	
<i>H. spinifrons</i>	2	Gammarids		Unidentified Nematodes	3
<i>Haloptilus longicornis</i>	5	<i>Ampelisca diadema</i>	1	Hydromedusae	1
<i>H. spiniceps</i>	2	<i>Bathyporeia pelagica</i>	1	Decapod larvae	42
<i>H. validus</i>	2	<i>Urothoe marina</i>	3	Cirripede larvae	3
<i>Arietellus setosus</i>	2	<i>Urothoe</i> sp.	2		
<i>Candacia aethiopica</i>	1	<i>Pontocrates arenarius</i>	1		
<i>C. armata</i>	2	<i>Melita</i> sp.	5		
<i>C. bipinnata</i>	2	<i>Gammarus olivii</i>	7		
<i>C. longimana</i>	14	<i>Gammarus</i> spp.	5		
<i>Paracandacia bispinosa</i>	12	<i>Dexamine spiniventris</i>	1		
<i>P. simplex</i>	200	<i>D. spinosa</i>	4		
<i>Candacia</i> sp.	1	<i>D. thea</i>	5		
<i>Acartia clausi</i>	1	<i>Apherusa mediterranea</i>	1		
<i>Oithona setigera</i>	3	Unidentified	5		
<i>Oncaea conifera</i>	39				
<i>Oncaea media</i>	13				
<i>O. mediterranea</i>	34				

Table 6. *Myctophum punctatum*. Seasonal occurrence of more abundant (> 1%) prey species in the diet (mean no. stomach⁻¹)

Prey	No. ind. stomach ⁻¹			
	Winter	Spring	Summer	Autumn
Copepods				
<i>Nannocalanus minor</i>	5.14	5.30	34.58	9.43
<i>Temora stylifera</i>	0.24	0.50	31.25	7.39
<i>Pleuromamma</i> sp.	1.29	6.10	7.75	4.51
<i>Pleuromamma abdominalis</i>	3.19	5.60	1.33	3.90
<i>Pleuromamma gracilis</i>	2.67	1.60	4.75	2.28
<i>Euchaeta marina</i>	0.52	–	10.33	1.60
<i>Euchirella messinensis</i>	0.29	0.20	0.08	3.42
<i>Paracandacia simplex</i>	0.29	0.30	1.17	2.64
<i>Neocalanus gracilis</i>	0.52	1.10	0.75	0.93
<i>Lucicutia flavicornis</i>	0.10	0.10	0.17	0.90
<i>Clausocalanus lividus</i>	1.43	0.10	–	0.45
<i>Clausocalanus parapergens</i>	0.48	0.40	0.08	0.63
Unidentified	22.05	23.10	94.25	44.19
Euphausiids				
<i>Meganyctiphanes norvegica</i>	8.24	0.50	–	0.03
<i>Euphausia krohnii</i>	0.24	2.60	1.17	0.03
Unidentified	8.86	3.20	1.17	0.31

first set of variable and observation scores was 0.777 and the correlation of the second set was 0.414. F1 opposed euphausiids with copepods while the other taxa were located near its mid-point. Little scattering of the variable-points was observed in the space of F2, except for chaetognaths that were located at its positive pole. Observation-points were arranged along F1 in a quasi-linear fashion. The model did not indicate a clear seasonal trend though a number of winter observations were concentrated near the euphausiid pole. Regression analysis demonstrated that F1 was linearly and significantly correlated with prey biomass ($r = -0.545$), prey taxa number ($r = -0.399$), prey diversity ($r = -0.642$) and fish size ($r = -0.33$).

An RQ analysis was also performed on a copepod population of 70 species observed in both *Hygophum benoiti* and *Myctophum punctatum* of intermediate size (40 to 50 mm) in all 4 seasons. This was done in order to avoid any bias due to fish size. Fig. 4 shows the ordination model in the plane of the first two factors. *H. benoiti* had a uniform diet as compared to the more mixed diet observed in *M. punctatum*. Two distinct seasonal trends were evident: both species fed on different prey populations in winter (and spring for *H. benoiti*) but their diet overlapped the rest of the year. Opposed 'feeding fields' (i.e. groups of species in opposite areas of the factorial space) were characterized by *Nannocalanus minor*, *Clausocalanus parapergens*, and *C. lividus* for *M. punctatum* in winter, and *Pleuromamma gracilis*, *Pleuromamma* sp. and *Oncaea mediterranea* for *H. benoiti* in this same period. Species characteristic of the common 'feeding

field' (species common to both predators) were *Pleuromamma gracilis*, *Neocalanus gracilis*, *Euchaeta marina*, *Lucicutia flavicornis*, and *Temora stylifera*.

DISCUSSION

Diet analysis of stranded *Hygophum benoiti* and *Myctophum punctatum* revealed a number of general features on the feeding ecology of both fishes. Changes were generally observed in both size and taxonomic composition of the diet with age. The relationship between fish size and prey population parameters – such as size, biomass and diversity – were analyzed and conceptual models derived from the results obtained using RQ analysis (Fig. 3). Fig. 5 A shows that *H. benoiti* had a polarized feeding behavior with respect to different prey size classes; small individuals tended to feed almost exclusively on copepods, whereas larger ones shifted toward an euphausiid-based diet. Prey diversity and biomass of other zooplankton taxa was maximum in intermediate size classes when *H. benoiti* fed on a larger proportion of intermediate-sized prey such as amphipods, mysids and chaetognaths. This model implies not only a greater efficiency in capturing larger prey with increasing fish size but size selective feeding during all stages of the life cycle. *M. punctatum*, on the other hand, had a mixed diet during all stages of its development, except for small individuals that fed almost exclusively on copepods (Fig. 5 B). Though this trend was irregular, diversity and biomass of the prey items generally

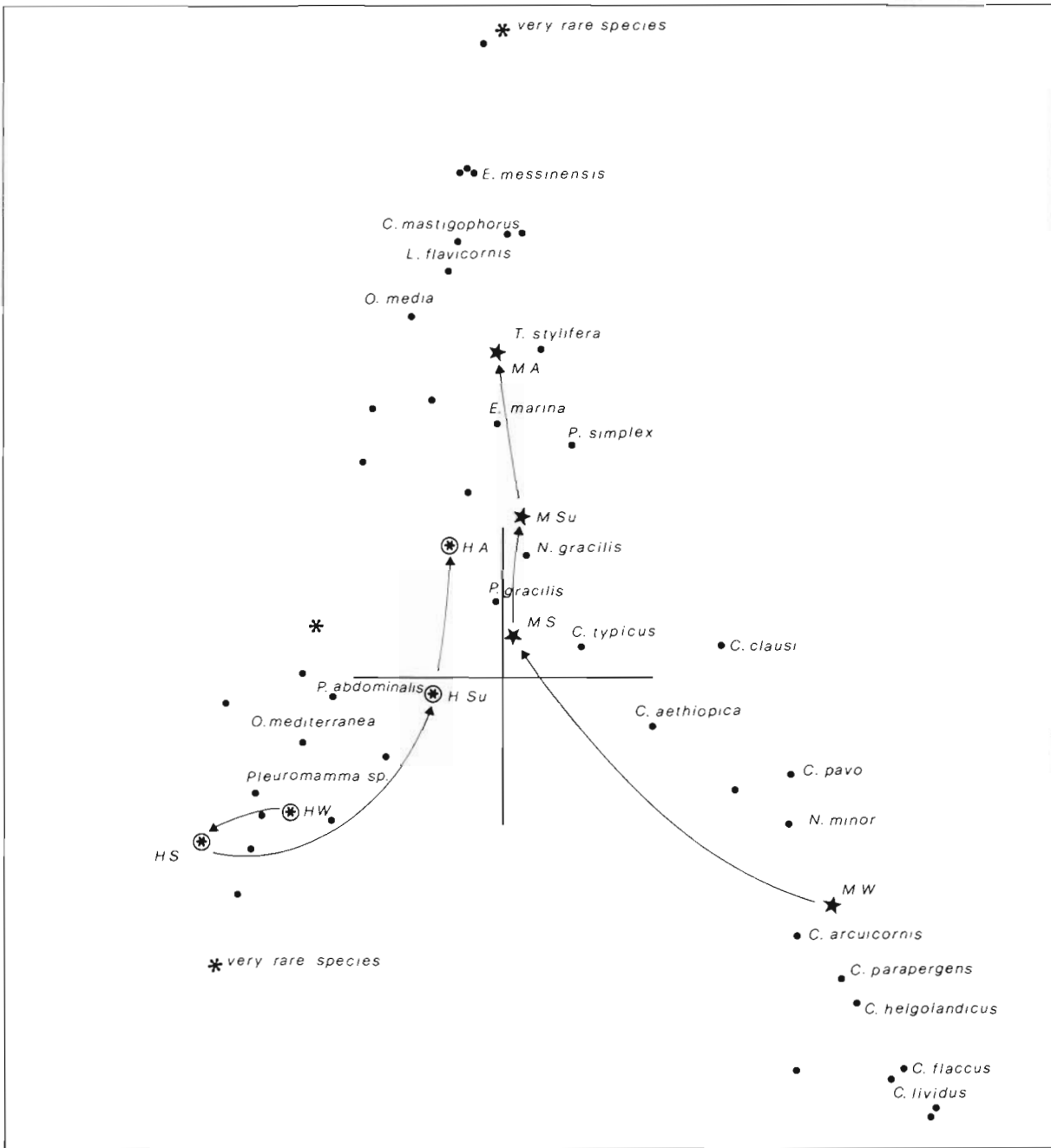


Fig. 4. RQ Analysis: Ordination model in the plane of the first two factors, showing seasonal trends in diet composition of the copepod prey population in intermediate *Hygophum benoiti* and *Myctophum punctatum* size classes (40 to 50 mm). Points: copepod species (only abundant species reported). ⊗ *H. benoiti* winter HW; spring HS; summer HSu; autumn HA. ★ *M. punctatum* winter MW; spring MS; summer MSu; autumn MA

increased with increasing fish size. This suggests that *M. punctatum* becomes a more opportunistic and efficient predator with age. Opportunistic feeding of this type, where larger individuals add components to their diets but do not exclude prey items eaten by smaller individuals, was also demonstrated for *Stenobranchius leucopsarus* and may represent the more common

feeding strategy for midwater fishes (Collard, 1970; Tyler and Pearcy, 1975). *M. punctatum* was also the more active predator, utilizing a broader range of food items such as gastropods, thaliaceans and appendicularians which were almost absent in the diet of *H. benoiti*. Furthermore, *M. punctatum* fed on almost twice the number of individuals as compared to *H.*

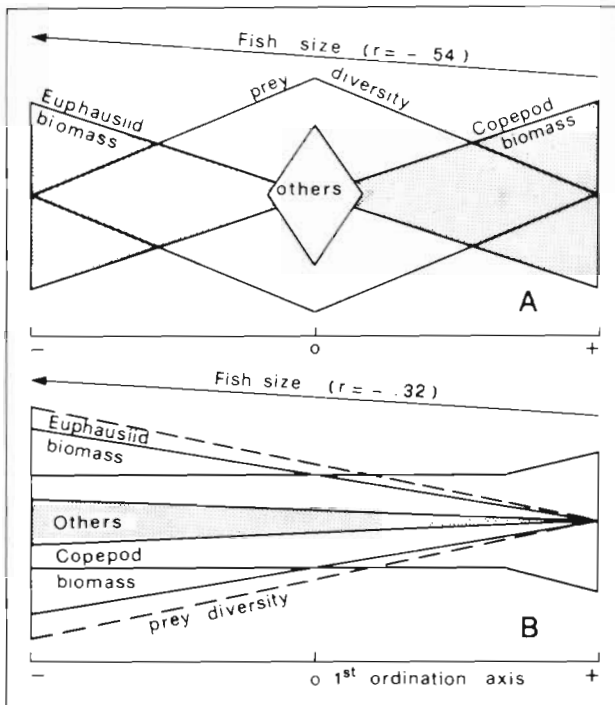


Fig. 5. Conceptual model of the relationship between fish size and prey size, biomass and diversity in (A) *Hygophum benoiti* and (B) *Myctophum punctatum* (r = correlation coefficient between fish size and first axis of the ordination model)

benoiti (1.47 times more in terms of biomass). This may imply higher absolute energy requirements.

The data available on net zooplankton of the Straits of Messina, which includes day-night zooplankton sampled in various areas of the Straits at discrete levels from 500 m to the surface (own unpubl. data), provide evidence that the faunistic composition and vertical distribution of individual species are similar to those recorded for other Mediterranean waters such as the Tyrrhenian and Adriatic Seas (Hure and Scotto di Carlo, 1968, 1969a). Since the turbulence associated with upwelling may not affect the overall structure of the zooplankton community of the Straits, knowledge on prey distribution patterns can furnish valuable information on depth and time of feeding of the predators. The stomach contents of both *Hygophum benoiti* and *Myctophum punctatum* were heavily dominated by copepods and euphausiids. Abundant food items included typical surface species such as the copepods *Nannocalanus minor*, *Temora stylifera* and *Euchaeta marina*, and intermediate-water species that undergo strong diel migrations reaching the surface at night such as the copepods *Pleuromamma gracilis* and *P. abdominalis* and the euphausiids *Meganyctiphanes norvegica* and *Euphausia krohnii* (Hure, 1961; Casanova-Soulier, 1968; Hure and Scotto di Carlo,

1969b). Few intermediate and no deep water non-migrating species (i.e. species with day-night residence depths below 200 m) were recorded in the stomach contents indicating that both *H. benoiti* and *M. punctatum* had fed in surface waters at night. Both fishes fed more or less on the same prey species (Tables 2 and 4) but surface species prevailed in *M. punctatum* whereas migrating intermediate-water species were more common in *H. benoiti*. This suggests that the 2 fishes probably fed at slightly different depth levels. That is, *M. punctatum* may have fed at the near surface and *H. benoiti* at a somewhat lower depth. Distinct 'feeding fields' were in fact demonstrated when an RQ analysis was performed on a homogeneous prey population (copepods) using only one predator size class (Fig. 4). Overlapping of the diet, however, occurred in summer and autumn reflecting low prey diversity in the surrounding waters at this time (see also Hure and Scotto di Carlo, 1968) and consequently a greater probability of capturing the same prey species.

Seasonal differences in the diet reflected predator size-distribution patterns and taxonomic composition of the prey population at the time of feeding. It follows that the relative abundance of larger prey items such as euphausiids occurred in winter in *Myctophum punctatum* and summer in *Hygophum benoiti* when both species respectively reached their maximum size. Feeding on the same food type in different periods of the year may reduce competition for available resources in these 2 cohabiting fishes. At the species level, however, changes in diet composition may simply reflect prey availability in different periods of the year. Species were in fact preyed upon by both predators in a larger proportion when they reached peak abundances in the surrounding waters (e.g. *Temora stylifera* and *Euchaeta marina* in summer and autumn; *Oncaea mediterranea*, *Clausocalanus lividus* and *Meganyctiphanes norvegica* in winter; *Euphausia krohnii* in spring and summer). Nevertheless, the species assemblage in the stomachs did not exactly reflect the zooplankton population at the time of feeding. Small dominant copepods (about 1 mm) such as *Clausocalanus furcatus* and *Ctenocalanus vanus* were rarely consumed. Excluding size selection due to gill raker spacing (Ebeling and Cailliet, 1974), this suggests visually oriented predation on appropriate size classes and probably stronger feeding pressure on more visible organisms (Confer et al., 1978). Preferential feeding on the genus *Pleuromamma* has been reported by several authors (Hopkins and Baird, 1973, 1977; Merrett and Roe, 1974; Clarke 1978, 1980; Baird and Hopkins, 1981). Our results suggest that selective feeding occurred not only on the genus *Pleuromamma* but on other bioluminescent copepods such as *Nan-*

nocalanus minor and *Neocalanus gracilis* (Tett and Kelly, 1973) which were preyed upon in a larger proportion than their absolute abundance in surrounding waters. For these copepods the adaptive significance of bioluminescence therefore does not seem to involve predator avoidance mechanisms. Prey choice, however, may also involve aggregation or patchy distribution of food items as demonstrated by the presence of a monospecific and even monosexual prey population in the stomachs of several *H. benoiti* and *M. punctatum* (e.g. 119 male and 1 female specimens of the copepod *T. stylifera* were the only food items in 1 *M. punctatum* specimen).

Can the results obtained from stomach contents analyses give insight into the mechanisms involved in the shore stranding of these 2 species? Current opinion emphasizes physical factors, namely strong vertical currents in the Straits, as the main cause involved in the passive transport of midwater organisms to the surface and under favorable wind conditions these organisms are then washed ashore.

Though stranding frequency is maximum in autumn and winter when SE winds are stronger and more frequent, our results provide evidence that for *Hygophum benoiti* and *Myctophum punctatum*, at least, physical factors may have a minor role in this phenomenon. This assumption is based on the facts that:

(1) Individuals below 21 mm for *H. benoiti* and 22 mm for *M. punctatum* were never found stranded. Excluding any bias in sampling smaller individuals, we can assume that juveniles do not strand. If the vertical passive transport hypothesis were to hold true, small size classes, less capable of actively opposing vertical currents, would be much more frequent in stranded material. The greater swimming capacity of larger individuals is demonstrated by the fact that they capture such large and fast-moving prey items as euphausiids.

(2) No everted stomachs were found in *Hygophum benoiti* or *Myctophum punctatum*. Stomach eversion from distended swim bladders is well known in midwater fishes when they undergo rapid decompression of the type implied by the vertical passive transport hypothesis

(3) Few empty stomachs were recorded (5 for *Myctophum punctatum* and 14 for *Hygophum benoiti*) and the contents were generally poorly digested. Contents analyses revealed that only surface or sub-surface migrating elements had been eaten indicating that stranded fishes were feeding near the sea-surface. Should the vertical passive transport hypothesis hold true, one would expect to find deep water non-migrating zooplankters in the prey population, either fed upon in their normal habitat or in surface waters. There

is no reason to believe that differential passive transport applies to predators and their prey.

The above considerations suggest that *Hygophum benoiti* and *Myctophum punctatum* are strong vertical migrators that feed on surface zooplankton communities. Such trophic migrations most probably occur at night when both fishes are known to reach the surface layers (Goodyear et al., 1972; Nafpaktitis et al., 1977). The diet composition strongly resembles a nocturnal zooplankton community in surface waters, consisting of both surface and migrating sub-surface species. It is worth noting, however, that while *H. benoiti* migrates only in open waters, *M. punctatum* may also intrude to near-shore environments as demonstrated by the presence in the stomach contents of benthoplankters inhabiting shallow, soft-bottom waters. Seemingly, trophic migrations involve only adult populations of both species. Differences in stranding frequency recorded for males and females may be due to differences in migrating behaviour.

Stranding of these lanternfishes probably occurs during or after feeding when fish are caught in surface eddies formed by opposing tidal currents and pushed ashore by onshore SE winds. The stranding mechanisms discussed above may not (and probably do not) necessarily apply to other stranded midwater organisms which include non-migrants such as fish species of the genus *Cyclothone* and weak migrants such as *Argyropelecus hemigymnus*. In conclusion, we believe that there is no univocal explanation of this phenomenon since each species will react differently to the same environmental stress, depending on the biology of the single species. Stomach contents analyses may, however, serve as a valuable tool in reconstructing the mechanisms involved in the stranding of these species.

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