

## Research Article

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**Cite this article:** Sassa C, Takahashi M, Tsukamoto Y (2023). Diet composition, diel feeding periodicity and daily ration of mature adult *Diaphus fulgens* (Teleostei: Myctophidae) in the Kuroshio waters. *Journal of the Marine Biological Association of the United Kingdom* **103**, e48, 1–11. <https://doi.org/10.1017/S002531542300036X>

Received: 18 November 2022

Revised: 26 April 2023

Accepted: 31 May 2023

### Keywords:

appendicularians; daily caloric intake; daily ration; diel feeding periodicity; diet composition; multiple batch spawner; myctophids

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# Diet composition, diel feeding periodicity and daily ration of mature adult *Diaphus fulgens* (Teleostei: Myctophidae) in the Kuroshio waters

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## Abstract

*Diaphus fulgens* is a diel vertical migrant myctophid, occurring abundantly in the Kuroshio waters of the East China Sea. They are multiple batch spawners with a short interspawn period, resulting in high egg productivity. Multiple spawning would be supported by feeding during their spawning season; however, there is no information on the feeding habits of this species. The present study examined the diet composition, diel feeding periodicity and daily ration of mature adult *D. fulgens* collected at different periods of the day during February to March. The most prevalent item was appendicularians and their mucus houses, which dominated the stomach contents in both number and weight. Additionally, various species of copepods were predated, with a prevalence, by weight, of the large-sized *Pleuromamma piseki*. *Diaphus fulgens* feeds actively in the epipelagic layer at night and moves down to the mesopelagic layer in the early morning, and digests most of the consumed food by the late afternoon, showing a typical nocturnal feeding pattern. Based on diel changes in the stomach content index and instantaneous gastric evacuation rate estimated in this study ( $0.118\text{--}0.129\text{ h}^{-1}$ ), the daily ration was calculated to be  $4.0\text{--}4.2\%$  of body weight, equivalent to a daily caloric intake of  $21.2\text{--}22.3\text{ cal day}^{-1}$ . Since the caloric value to produce a batch of oocytes was estimated to be  $8.2\text{--}11.5\text{ cal day}^{-1}$ , on an energetic basis, *D. fulgens* can maintain the multiple spawning at a cost of approximately  $37\text{--}54\%$  of its daily caloric intake.

## Introduction

Recent estimates suggest that the global biomass of mesopelagic fishes could be the order of 9–19.5 gigatonnes (Irigoin *et al.*, 2014; Proud *et al.*, 2017, 2019), roughly equivalent to 100 times the annual tonnage captured worldwide by commercial fishing (Hidalgo and Browman, 2019; FAO, 2022). Myctophids (members of the family Myctophidae) are one of the most important members of mesopelagic fishes in the world's oceans both in terms of abundance and biomass (Gjøsæter and Kawaguchi, 1980; Brodeur and Yamamura, 2005). They are distributed throughout the oceans from subarctic and Antarctic to tropical waters, and from waters over continental shelves and slopes to the open oceans, and include 249 species in 32 genera (Priede, 2017). The ecological roles of myctophids in the oceanic ecosystems are recognized as a critical mid-trophic level that transfers energy from the zooplankton to upper trophic levels, mainly because of their huge biomass (Davison *et al.*, 2013; Choy *et al.*, 2016; Eduardo *et al.*, 2020).

The most remarkable biological and ecological feature of myctophids is their diel vertical migrations (DVM) between the mesopelagic and epipelagic layers (Clarke, 1973; Oozeki *et al.*, 2012; Sutton, 2013). The DVM of myctophids has been regarded as an upward feeding migration from the mesopelagic layer into the productive epipelagic layer at night (Hopkins and Baird, 1985; Williams *et al.*, 2001; Dypvik and Kaartvedt, 2013). Also, nighttime feeding in the epipelagic layer has been considered to be an adaptive response to escape from visual epipelagic predators such as larger fishes, squids, sea birds and marine mammals (Robison, 2003; Brodeur and Yamamura, 2005). Main prey items of myctophids are crustacean zooplankton (Gartner *et al.*, 1997; Pusch *et al.*, 2004b; Drazen and Sutton, 2017), while some myctophid species feed mainly on gelatinous plankton (Takagi *et al.*, 2009; Bernal *et al.*, 2015; Sassa and Takasuka, 2020). Based on analyses of diel changes in the stomach contents (SC), daily rations (DR) of myctophids have been shown to range from approximately 0.4 to 5.9% of the body weight per day (Moku and Hidaka, 2002; Pusch *et al.*, 2004a; Tanaka *et al.*, 2013; Drazen and Sutton, 2017; Contreras *et al.*, 2020), although information on the DR is still limited for this family.

Various myctophid species are reported to be multiple batch spawners with relatively short interspawn periods, usually within several days, and show high relative batch fecundities of  $480\text{--}870\text{ eggs g}^{-1}$  (Lisovenko and Prut'ko, 1987; Gartner, 1993; García-Seoane *et al.*, 2014; Sassa *et al.*, 2016; Sarmiento-Lezcano *et al.*, 2020). Egg production of myctophids is considered to be at a similar level as that of anchovies (*Engraulis* spp.), one of the most active multiple spawners (Alheit, 1993; Sassa, 2019; Caiger *et al.*, 2021).

*Diaphus fulgens* is a small-sized myctophid [maximum standard length (SL) of approximately 45 mm] and broadly distributed in subtropical–tropical waters of the Indo-Pacific, being one of the most abundant species in the genus *Diaphus* in the Kuroshio waters (Wisner, 1976; Kawaguchi and Shimizu, 1978; Nafpaktitis, 1978). They perform DVM from the mesopelagic layer between 400 and 600 m during the day up to the epipelagic layer between 20 and 200 m at night (Kawaguchi and Shimizu, 1978; Ohizumi *et al.*, 2001). The multiple batch spawner *D. fulgens* actively spawns in the Kuroshio waters of the East China Sea (ECS) during late winter (Sassa and Takahashi, 2022). Spawning interval of this species is estimated to be 3–4 days, with a mean relative batch fecundity of 726 eggs g<sup>-1</sup> (Sassa and Takahashi, 2022). The high egg productivity of *D. fulgens* would be supported by feeding during the spawning season, as suggested for some species of this family (Gartner, 1993; Sassa *et al.*, 2016; Sassa and Takasuka, 2019); however, there is no information on the feeding ecology of this species to assess this hypothesis.

The present study described the diet composition, diel feeding periodicity and DR of mature adult *D. fulgens* in the Kuroshio waters of the ECS during the spawning season. Estimated daily caloric intake was compared with the caloric value to produce a batch of oocytes to discuss the energy budget required to sustain multiple spawning.

## Materials and methods

### Sample collection

*Diaphus fulgens* were collected at 89 stations in the Kuroshio waters from the slope region to the Okinawa Trough in the ECS during February to March in 2008 and from 2012 to 2017 onboard either the RV 'Yoko-Maru' (Japan Fisheries Research and Education Agency) or 'Kaiyo-Maru No. 7' (Nippon Kaiyo Co. Ltd.) (Figure 1, Table 1). The specimens were collected over almost the whole distribution depth range during different hours of both the day and night. In 2008, a midwater otter trawl (25 × 25 m mouth opening; 9 mm mesh of cod end) tow was conducted for 30 min horizontally during the nighttime (2200–0400 h) in the epipelagic layer between 30 and 60 m depth (Table 1). A Matsuda–Oozeki–Hu trawl (MOHT, 2.24 × 2.24 m mouth opening; 1.59 mm mesh net) (Oozeki *et al.*, 2004) was obliquely towed from the surface to 152 ± 3 m [mean ± standard deviation (SD)] at night in 2012 and from the surface to 518 ± 45 m (mean ± SD) regardless of day or night during 2013–2017 (Table 1). Mean towing duration (±SD) of the MOHT was 38 ± 4 min in 2012 and 58 ± 12 min during 2013–2017. In 2013, a small-sized midwater trawl [larval catcher net (LC net, Tokyo, Japan), Nichimo Co. Ltd., 8 × 8 m mouth opening; 9 mm mesh net] was towed during the daytime for 40–60 min in the mesopelagic layer between 400 and 600 m depth where the deep scattering layers were observed (Table 1). During all tows, net depth was monitored acoustically using a trawl monitoring system (Scanmar AS, Åsgårdstrand, Norway). Samples were fixed in 10% buffered formalin-seawater or preserved in 99.5% ethanol at sea.

### Stomach content analysis

For 550 individuals, after SL and body wet weight (BW) were measured to the nearest 0.1 mm and 1 mg, respectively, stomachs were dissected, and the contents removed. Gonads of these individuals have already been analysed by Sassa and Takahashi (2022). Total wet mass of the SC was weighed to the nearest 0.01 mg for the 550 individuals to analyse the diel feeding periodicity and DR. In this study, stomachs were considered 'empty' if

the SC was <3 mg. SL of these individuals ranged from 24.3 to 43.1 mm, with a mean ± SD of 33.5 ± 2.1 mm (Figure 2), most of which have matured gonads based on histological examination (Sassa and Takahashi, 2022). The degree of stomach fullness was estimated by the stomach content index (SCI):

$$\text{SCI} = \frac{\text{SC}}{\text{BW}} \times 100. \quad (1)$$

To analyse the diet composition, for 75 individuals with SCI >1% collected at four nighttime sampling stations by the midwater otter trawl in 2008 (15–20 individuals at each station) (Figure 1, Table 1), SC were counted and identified to the lowest possible taxon, based on the keys of Chihara and Murano (1997). Diet composition in the present study should not be biased by incidental feeding in the cod-end after capture (i.e., net feeding) because of the adoption of a 9 mm mesh of cod end, which allowed most of the zooplankton prey to pass through. Total lengths and widths were determined to the nearest 0.01 mm under a microscope fitted with an ocular micrometer for each item for which body measurements were possible. Additionally, prosome lengths were measured for copepods; trunk lengths for appendicularians. The mean dimensions of each prey item were converted to the approximate dry weight (DW) based on equations from Uye (1982) and Anraku *et al.* (1986) for copepods, ostracods and decapods; Ikeda (1990) for amphipods; Iguchi and Ikeda (1995) for euphausiids; Tomita *et al.* (1999) for appendicularians; and Uye (1982), Anraku *et al.* (1986) and Uye *et al.* (1996) for the other taxa.

The modified index of relative importance (IRI), i.e., using DW rather than the wet weight (WW) of prey items, was calculated to characterize the diet and to rank prey taxa. The IRI was expressed as the percentage of total IRI (%IRI) for each prey item *i*:

$$\% \text{IRI}_i = \frac{(\%N_i + \%W_i) \times \%F_i}{\sum_{i=1}^n (\%N_i + \%W_i) \times \%F_i} \times 100, \quad (2)$$

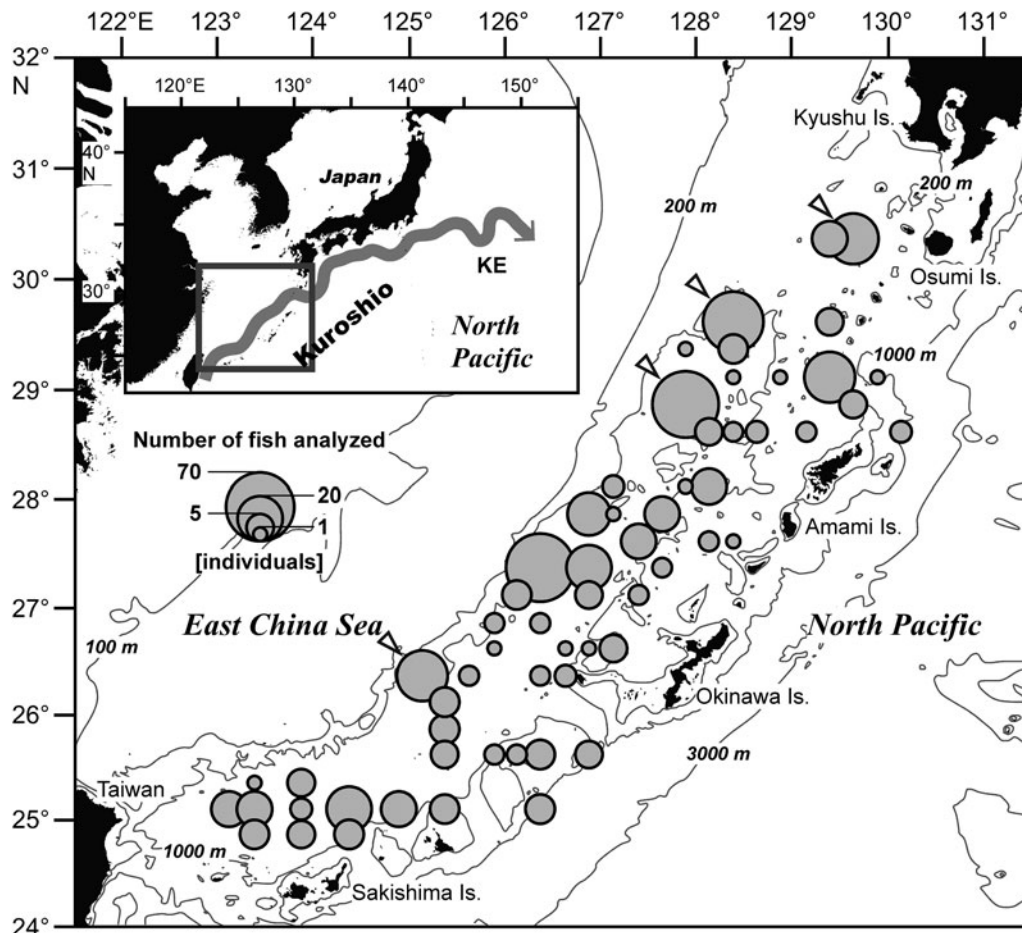
where %N<sub>*i*</sub> is the percentage of each prey item *i* to the total number of identifiable prey items, %W<sub>*i*</sub> is the percentage DW of each prey item *i* to the total DW of identifiable prey items, %F<sub>*i*</sub> is the frequency of occurrence of each prey item *i* in the total number of stomachs examined. To obtain a robust estimation of the relative importance of the prey, the results of diet composition should be reported as %N, %W, %F and %IRI for all taxa considered (Hyslop, 1980; Cortés, 1997).

The niche breadth of *D. fulgens* was based on Levins' standardized index ( $B_{\text{sta}}$ ; Levins, 1968):

$$B_{\text{sta}} = \frac{1}{(n-1)} \left( \frac{1}{\sum_{i=1}^n P_i^2} - 1 \right), \quad (3)$$

where  $P_i$  is the %IRI × 10<sup>-2</sup> of each prey item *i* in the diet, and *n* is the number of prey categories. This index ranges from 0 (the species consumes a single item) to 1 (the species exploits all available items in equal proportions).

The feeding strategy of *D. fulgens* was investigated based on the modified Costello (1990) graphical method (Amundsen *et al.*, 1996), plotting prey-specific abundance (*y*-axis) against %F (*x*-axis). The prey-specific abundance was defined as the number (or the weight) of prey item *i* divided by the total number (or the weight) of prey items in the stomachs that contained prey item *i*, expressed as a percentage. This method allows to infer information on the relative importance of the prey, feeding strategy and



**Figure 1.** Geographical distribution of *Diaphus fulgens* caught in the Kuroshio waters of the East China Sea in 2008 and 2012–2017. The number of individuals in each sampling location was combined within 30' × 30' (minute) of latitude and longitude. The size of circles indicates the number of fish examined at each site. Arrowheads indicate sampling locations where diet composition was examined. The total number of analysed specimens was 550. KE, Kuroshio Extension. Modified from Sassa and Takahashi (2022).

niche width contribution through the position of prey types along the diagonals and axes of the graph (Amundsen *et al.*, 1996).

**Estimation of daily ration**

In the present study, samples were collected on a 24 h basis. To analyse the diel feeding periodicity, the median and mean values of SCI were determined for the time periods of 2 h intervals from 0000 to 2400 h. The sunrise and sunset times during the samplings were approximately 0650–0705 and 1820–1850 h (local time), respectively. The SCI data sampled over 7 years were pooled to get enough data in each time period for producing a

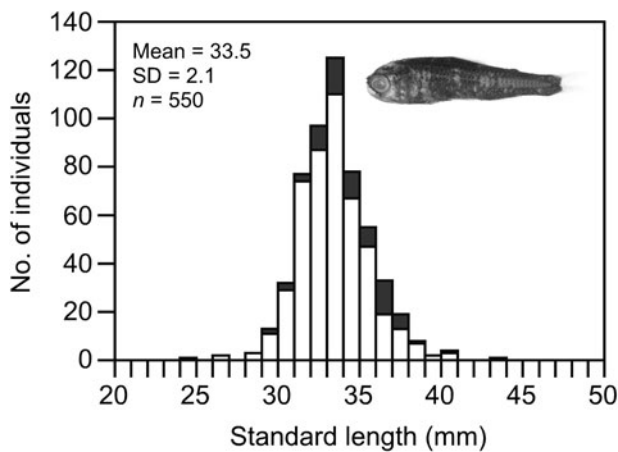
reliable result of diel feeding periodicity. We assumed no significant variation in the feeding habits among years in the Kuroshio waters where both physical oceanographic and biological conditions have been shown to be stable interannually (Watanabe *et al.*, 2002; Sugisaki *et al.*, 2010; Tadokoro *et al.*, 2022). Our objective is to describe the average feeding habits of *D. fulgens* during the spawning season.

DR of food was estimated based on the temporal change in SCI using the Elliott and Persson model (Elliott and Persson, 1978). This model assumes that SC decline exponentially with time, and feeding is constant within each specific and consecutive sampling time interval. Food consumption for each time interval can

**Table 1.** Sampling data for *Diaphus fulgens* in the Kuroshio region for the 7 years

Year	Date	Collecting gear	No. of stations	Depth (m)	Time	Total no. of <i>D. fulgens</i> sampled
2008 <sup>a</sup>	18 February–10 March	Midwater trawl	5	30–60	N	171*
2012 <sup>b</sup>	21 February–1 March	MOHT	10	0–152	N	57
2013 <sup>b</sup>	17–28 February	MOHT/LC net	5/5	0–508/400–600	N/D	14/100
2014 <sup>b</sup>	16–26 February	MOHT	21	0–506	ND	74
2015 <sup>b</sup>	18–28 February	MOHT	28	0–502	ND	96
2016 <sup>b</sup>	21–28 February	MOHT	9	0–602	ND	26
2017 <sup>b</sup>	23–26 February	MOHT	6	0–514	ND	12

The maximum depth to which the MOHT sampled was averaged for each year. \*Diet composition was analysed for 75 individuals collected at four nighttime sampling stations by the midwater otter trawl in 2008 (Figure 1). Research vessel: a, 'Kaiyo-Maru No. 7'; b, 'Yoko-Maru'. N, night; D, day.



**Figure 2.** Standard length (SL) frequency distributions of *Diaphus fulgens* examined. To estimate feeding rhythm and daily ration, total wet mass of the stomach contents was weighed for all individuals. Of these, 75 individuals were examined for diet composition (filled bars). *n*, total number of fish analysed.

be estimated by the following equation:

$$C_t = \frac{(S_t - S_{t-1})e^{-R \times t}}{1 - e^{-R \times t}}, \quad (4)$$

where  $C_t$  is the food consumption between time intervals  $t$  and  $t-1$ ,  $S$  is the median SCI at time intervals  $t$  and  $t-1$ ,  $t$  is the duration of each time interval in hours, i.e., 2 h and  $R$  is the instantaneous gastric evacuation rate ( $\text{h}^{-1}$ ). To perform accurately, the Elliott and Persson model requires that sampling intervals be 3 h or less (Elliott and Persson, 1978), and the present study meets this requirement. The DR was taken as the sum of  $C_t$  obtained for each interval during the period of active feeding.

$R$  was determined from SCI over a period of fasting after a period of heavy feeding by the following equation:

$$S_t = S_0 e^{-R \times t}, \quad (5)$$

where  $t$  is the time after fasting started,  $S_0$  is the median SCI value at the start of the fasting time interval ( $t = 0$ ) and  $S_t$  is the median SCI value at time interval  $t$ . In this study,  $R$  was estimated by a linear regression from the natural ln-transformed equation, using the data from the early morning (0400–0600 h or 0600–0800 h) to the late afternoon (1600–1800 h) when the SCI was declining (see results):

$$\ln S_t = \ln S_0 - R \times t. \quad (6)$$

To discuss the relationship between the daily caloric intake and energetic cost of multiple spawnings, food requirements ( $F$ ) of *D. fulgens* females based on the caloric value ( $\text{cal day}^{-1}$ ) were calculated using the following equation:

$$F = \overline{\text{BW}} \times \text{DR} \times 10^{-2} \times 0.2 \times 5.1, \quad (7)$$

where  $\overline{\text{BW}}$  is the mean BW of *D. fulgens* females (mg) and DR is the daily ration estimated (% of BW). Since mean BW ( $\pm$ SL) of female and male *D. fulgens* is  $520 \pm 126$  and  $513 \pm 119$  mg, respectively, in the specimens used in the present study (same specimens as used in Sassa and Takahashi, 2022), 520 was adopted as the value of  $\overline{\text{BW}}$ . A WW–DW ratio of 0.20 for mesozooplankton (Peters and Downing, 1984) was used. Proteins form the major biochemical component of zooplankton, including copepods and appendicularians, main prey items of *D. fulgens*

(Mayzaud and Martin, 1975; Harmelin-Vivien *et al.*, 2019). In the present study, the conversion factors in energy for proteins was assumed to be 5.1 cal ( $=21.4$  J) per 1 mg of DW of food, based on Postel *et al.* (2000) for zooplankton.

## Results

### Diet composition

Overall, 2263 prey items were found from the 75 stomachs examined. The maximum number of prey items per stomach (72 individuals) was found in an individual of 36.1 mm SL collected at 0200–0400 h. A total of 59 prey items were identified in the stomachs (Table 2), while Levins' standardized index  $B_{\text{sta}}$  had a markedly low value of 0.04 which indicates a restricted niche breadth, i.e., specialized feeding.

Appendicularians were one of the most important prey items in terms of %N, %W and %F (41.0, 24.8 and 65.3%, respectively), being the highest %IRI value of 48.6% (Table 2). Mean trunk length ( $\pm$ SD) of appendicularians eaten was  $750 \pm 230$   $\mu\text{m}$ . Additionally, appendicularian mucus houses showed high values of %N and %F (15.8 and 54.7%, respectively), resulting in %IRI values of 13.6%. Appendicularian houses were compressed as they pass through the oesophagus and stay in the stomach, which makes the size compact, with a mean length ( $\pm$ SD) of  $1266 \pm 411$   $\mu\text{m}$ .

Copepods included three orders, 19 genera and 44 species or species groups, having the highest species diversity among prey items (Table 2). In terms of %W, copepods were the most dominant prey items, accounting for the cumulative %W of 53.4% for total copepods. Of these, the large-sized copepods *Pleuromamma piseki* and *P. abdominalis* were important species, accounting for %IRI values of 6.9 and 4.2%, respectively. Mean prosome length ( $\pm$ SD) of these two species was  $1022 \pm 273$  and  $2047 \pm 438$   $\mu\text{m}$ , respectively. The importance of *P. piseki* would potentially be underestimated because of the considerable proportion of *Pleuromamma* spp. (%IRI = 10.2%) and Calanoida (%IRI = 8.3%), unidentifiable to the species level due to digestion, but can be considered as *P. piseki*, based on the similarity of the prosome length ( $1165 \pm 475$  and  $996 \pm 449$   $\mu\text{m}$ , respectively).

Based on the numerical Costello analysis, only appendicularians were located in the upper right quadrant, indicating a feeding specialization for this prey item (Figure 3A). Appendicularian houses, *Pleuromamma* spp., *P. piseki* and Calanoida were located in the lower right quadrant, contributing to a broader trophic niche breadth, although the contribution to the overall diet was limited. The other prey items were located in the lower left quadrant of the graph (Figure 3A), showing that they occurred rarely and were of relatively low importance to the overall diet. Based on the Costello analysis by weight, appendicularians, appendicularian houses, *Pleuromamma* spp., *P. piseki* and Calanoida were located in the lower right quadrant, showing a similar trend to the numerical analysis (Figure 4B). The other prey items were located in the lower left quadrant of the graph, although *Pleuromamma abdominalis*, *P. xiphias* and *Euchaeta rimana* showed relatively high values of prey-specific abundance (Figure 4B). These three species were consumed rarely, but when they were consumed accounted for a large proportion of the diet by weight.

### Diel feeding periodicity

Diel change in the percentage of empty stomachs and the SCI revealed a clear feeding periodicity (Figure 4). The percentage of empty stomachs increased gradually from the lowest values of 1.6% in the early morning (0400–0600 h) to the highest

**Table 2.** Summary of prey items in *Diaphus fulgens* in the Kuroshio waters of the East China Sea during late winter in 2008

Phylum/class/order	Species/taxon	%N	%W	%F	%IRI
Polychaeta	Polychaeta unid.	0.06	<0.01	1.33	<0.01
Ostracoda	<i>Conchoecia</i> spp.	1.65	2.20	24.00	1.04
Copepoda	Nauplius	0.24	0.15	5.33	0.02
	<i>Acrocalanus gracilis</i>	0.06	0.05	1.33	<0.01
	<i>Acrocalanus monachus</i>	0.06	0.03	1.33	<0.01
	Aetideidae unid.	0.06	0.07	1.33	<0.01
	<i>Aetideus acutus</i>	0.12	0.14	2.67	<0.01
	<i>Aetideus</i> sp.	0.06	0.06	1.33	<0.01
	Calanidae unid.	0.12	0.23	2.67	0.01
	Calanoida unid.	6.99	5.01	61.33	8.32
	<i>Candacia bipinnata</i>	0.06	0.26	1.33	<0.01
	<i>Candacia tuberculata</i>	0.06	0.10	1.33	<0.01
	<i>Candacia</i> sp.	0.24	0.16	4.00	0.02
	<i>Clausocalanus furcatus</i>	0.06	0.02	1.33	<0.01
	<i>Cosmocalanus darwini</i>	0.12	0.19	1.33	<0.01
	<i>Eucalanus</i> sp.	0.06	0.06	1.33	<0.01
	<i>Euchaeta rimana</i>	0.82	4.40	9.33	0.55
	Euchaetidae unid.	1.29	4.14	14.67	0.90
	<i>Euchirella messinensis indica</i>	0.12	0.48	1.33	<0.01
	<i>Lucicutia flavicornis</i>	2.41	1.04	32.00	1.25
	<i>Lucicutia</i> spp.	0.41	0.14	9.33	0.06
	<i>Mesocalanus tenuicornis</i>	0.06	0.14	1.33	<0.01
	Paracalanidae unid.	0.24	0.07	5.33	0.02
	<i>Paracalanus parvus</i> s.l.	0.18	0.04	4.00	<0.01
	<i>Paracandacia bispinosa</i>	0.06	0.10	1.33	<0.01
	<i>Paracandacia simplex</i>	0.12	0.10	2.67	<0.01
	<i>Paracandacia truncata</i>	0.41	0.67	6.67	0.08
	<i>Paraeuchaeta concinna</i>	0.18	0.51	4.00	0.03
	<i>Paraeuchaeta plana</i>	0.12	0.30	2.67	0.01
	<i>Pleuromamma abdominalis</i>	1.76	12.02	26.67	4.16
	<i>Pleuromamma gracilis</i>	0.65	0.74	10.67	0.17
	<i>Pleuromamma indica</i>	0.24	0.37	5.33	0.04
	<i>Pleuromamma piseki</i>	7.52	5.83	45.33	6.85
	<i>Pleuromamma xiphias</i>	0.59	6.89	10.67	0.90
	<i>Pleuromamma</i> spp.	7.11	8.30	58.67	10.22
	<i>Temora discaudata</i>	0.06	<0.01	1.33	<0.01
	<i>Undeuchaeta plumosa</i>	0.06	0.09	1.33	<0.01
	<i>Oithona</i> spp.	0.24	0.03	5.33	0.02
	<i>Corycaeus furcifer</i>	0.06	0.01	1.33	<0.01
	<i>Corycaeus</i> sp.	0.06	<0.01	1.33	<0.01
	<i>Oncaea media</i>	0.12	<0.01	2.67	<0.01
	<i>Oncaea mediterranea</i>	0.94	0.16	17.33	0.22
	<i>Oncaea scottodicarloi</i>	0.06	<0.01	1.33	<0.01
	<i>Oncaea venusta</i>	1.70	0.25	29.33	0.65
	<i>Oncaea waldemari</i>	0.06	<0.01	1.33	<0.01
	<i>Oncaea</i> spp.	0.59	0.06	9.33	0.07

(Continued)

**Table 2.** (Continued.)

Phylum/class/order	Species/taxon	%N	%W	%F	%IRI
	<i>Triconia conifera</i>	0.29	0.07	6.67	0.03
Amphipoda	Hyperideida unid.	0.41	1.96	6.67	0.18
Euphausiacea	Calyptopsis	0.47	0.09	9.33	0.06
	Furcilia	0.35	0.15	5.33	0.03
	<i>Euphausia</i> sp.	0.06	1.51	1.33	0.02
	Euphausiidae unid.	0.18	0.30	2.67	0.01
Decapoda	<i>Lucifer</i> sp.	0.06	0.05	1.33	<0.01
Chaetognatha	Chaetognatha unid.	0.94	0.88	13.33	0.27
Appendicularia	Appendicularia unid.	41.01	24.79	65.33	48.62
	Appendicularian house	15.80	6.16	54.67	13.58
Teleostei	Larval fish	0.12	0.86	2.67	0.03
	Fish scale	1.53	0.25	21.33	0.43
Others	Crustacean fragments	0.59	7.29	12.00	1.07

%N is the numerical percentage, %W is the dry weight percentage, %F is the frequency of occurrence percentage of fish with prey item *i* and %IRI is the percentage of total IRI (index of relative importance) for all prey taxa.  $IRI = (\%N + \%W) \times \%F$ .

value of 55.0% in the late afternoon (1600–1800 h) (Figure 4A). Then, the values declined sharply to 15.8% between 1800 and 2200 h and continued to decline gradually until the early morning (0400–0600 h).

Median SCI fluctuated between 0.49 and 2.19% over 24 h, and its diurnal variation showed a reverse pattern to that of the percentage of empty stomach (Figure 4B). The SCI began to increase just after sunset from 1800 to 2000 h, then maintained at high median values of 1.16–1.24% from 2000 to 0400 h. The median SCI peaked (2.18–2.19%) in the early morning (0400–0800 h). Then, it gradually decreased throughout the day, reaching its lowest value of 0.49% in the late afternoon (1600–1800 h).

### Daily ration

*R* was estimated assuming that the fasting period starts during the early morning (0400–0800 h) and ends in the late afternoon (1600–1800 h), when the SCI was declining (Figure 4). To show the possible range of the *R*, this study assumed two cases of the start period of fasting, i.e., 0400–0600 h or 0600–0800 h when the lowest value of the percentage of empty stomachs and the highest value of the median/mean SCI were observed, respectively. Data from these periods were fitted to the ln-transformed exponential function, and *R* was estimated to be 0.118–0.129 h<sup>-1</sup> (Figure 5).

To estimate the DR, the median SCI during the period of active feeding (1800–0800 h) was used. Based on the model, the DR was estimated to be 4.0–4.2% of BW. Using the estimated variables of DR, food requirement per *D. fulgens* female was estimated as 21.2–22.3 cal day<sup>-1</sup> in the Kuroshio waters of the ECS.

## Discussion

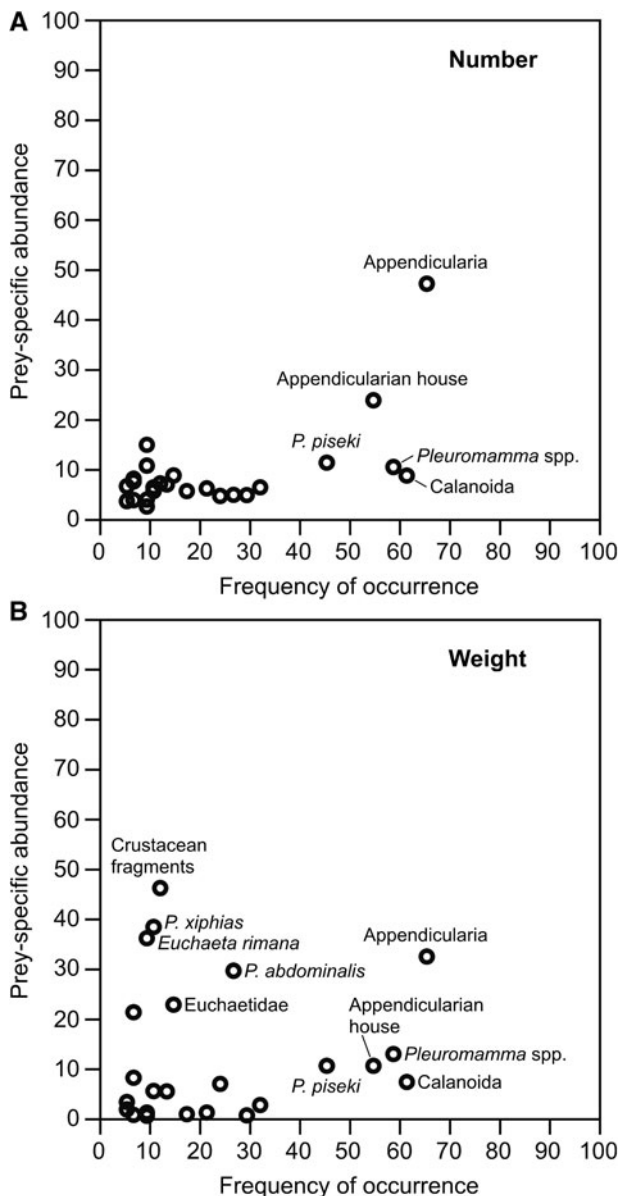
### Diet composition

Crustacean zooplankton such as copepods, ostracods, amphipods and euphausiids are major prey items for various species of myctophids in the world's oceans (Clarke, 1978; Hopkins and Gartner, 1992; Moku *et al.*, 2000; Shreeve *et al.*, 2009; Hudson *et al.*, 2014). In addition, dominance of gelatinous plankton, such as pteropods, salps, doliolids, appendicularians, in the stomachs of myctophids has been reported in the Kuroshio waters

(Watanabe *et al.*, 2002; Takagi *et al.*, 2009; Sassa and Takasuka, 2020) and other oceans (Baird *et al.*, 1975; Kinzer, 1982; Shreeve *et al.*, 2009; Bernal *et al.*, 2015). In the present study, the most prevalent prey item of *D. fulgens* was appendicularians, which dominated the SC both in number and weight. It should be noted that the %IRI values of appendicularians could be underestimated due to higher rate of digestion relative to crustacean prey items (Arai *et al.*, 2003). Although appendicularians have a high water content relative to their organic content, considering the rapid rate of digestion, appendicularians are potentially as significant an energy source for myctophids as crustacean zooplanktons.

The second most important prey items were appendicularian mucus houses. Assuming that *D. fulgens* ate the houses together with the appendicularian bodies, the size of the intact houses was estimated to be about 3000 µm based on the mean trunk length of 750 µm (Alldredge, 1976); thus, the size of the houses in the stomach (mean 1266 µm) was significantly compressed. Meanwhile, it is also possible that *D. fulgens* preyed selectively on discarded appendicularian houses in the water column. The relatively high %F (approximately 10–30%) of small-sized copepods of *Oncaea* possibly relates to the feeding on discarded appendicularian houses, since there are observations of attachment to and feeding behaviour of *Oncaea* on the discarded houses (Green and Dagg, 1997). The discarded appendicularian houses contain large amounts of organic materials, such as phytoplankton, protozoans and appendicularian fecal pellets (Alldredge, 1976), which is a component of marine snow (Lombard and Kjørboe, 2010).

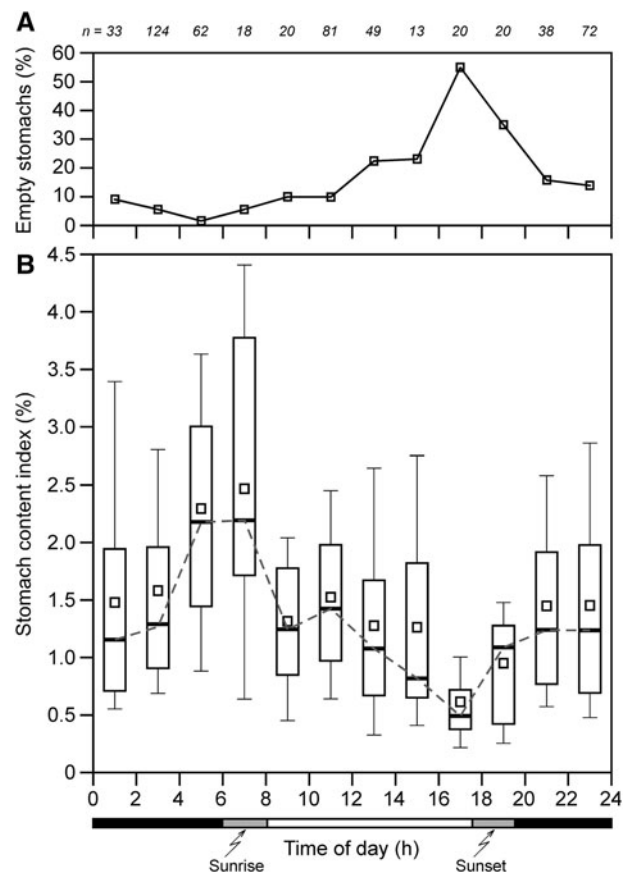
A large proportion of appendicularians occurs in the upper 100 m layer during both day and night without any clear DVM (Tomita *et al.*, 2003). In the Kuroshio waters, adult myctophids of *Myctophum asperum*, *Ceratoscopelus warmingii*, *Diaphus perspicillatus* and *D. suborbitalis* actively feed on appendicularians and their houses at night (Takagi *et al.*, 2009; Sassa, unpublished data). Juveniles of *M. asperum* and *M. orientale* also depend heavily on small-sized appendicularians of mean trunk length (±SD) of 563 ± 161 µm in the Kuroshio waters (Watanabe *et al.*, 2002; Sassa and Takasuka, 2020). Furthermore, Sassa and Kawaguchi (2004) reported that *Diaphus garmani* larvae fed mainly on small-sized appendicularian houses with a mean length of 450 ± 181 µm in the Kuroshio waters, while appendicularian bodies were rarely detected in their guts. In the present study, the mean size of the



**Figure 3.** Modified Costello–Amundsen plots showing relationships between prey-specific abundance, expressed as (A) number and (B) weight, and frequency of occurrence of prey items in the diet of *Diaphus fulgens* collected in the Kuroshio waters of the East China Sea in 2008.

appendicularians and their houses found in the stomachs of *D. fulgens* adults was 750 and 1266  $\mu\text{m}$ , respectively, which was significantly larger than those eaten by larval and juvenile myctophids. These observations indicate that various sizes of appendicularians and their houses provide a broad size spectrum of prey items, being a key taxon for myctophids during ontogeny in the Kuroshio waters. The trophic pathway of the tunicate food chain, linking pico-nanophytoplankton with fishes via appendicularians (Okazaki *et al.*, 2019), would be critical for myctophids in the oligotrophic Kuroshio region.

In the present study, copepods of the genus *Pleuromamma* dominated the SC of *D. fulgens* by weight. Vertical migrating *Pleuromamma* spp. have been reported as preferred prey items for various species of myctophids (Hopkins and Baird, 1985; Pusch *et al.*, 2004b; Takagi *et al.*, 2009; Dypvik and Kaartvedt, 2013; Bernal *et al.*, 2015; Battaglia *et al.*, 2016). In the present study, *P. piseki* was the most important copepod in terms of both %W and %F. *Pleuromamma piseki* occurs in the 400–500 m layer during the daytime and migrates to the upper 200 m

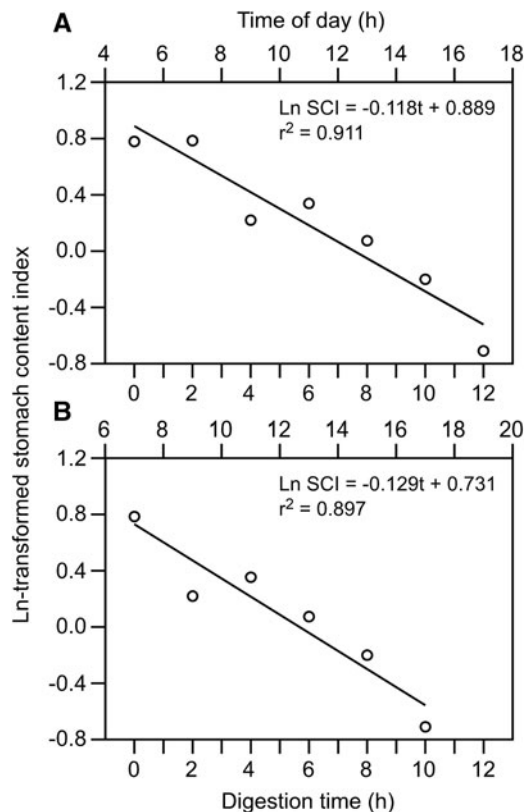


**Figure 4.** Diurnal changes in (A) the percentage of empty stomachs and (B) the stomach content index (SCI) of *Diaphus fulgens*. Data of the same diel time period from different years were pooled. The box plots denote median values and 25 and 75% interquartiles; the lower and upper whiskers represent 10 and 90% interquartiles; while squares represent the means. The sunrise and sunset times during the sampling were approximately 0650–0705 and 1820–1850 h (local time), respectively. *n*, total numbers of fish analysed for each time period.

layer during the nighttime (Ambler and Miller, 1987; Haury, 1988), showing a similar DVM to *D. fulgens* (Kawaguchi and Shimizu, 1978; Ohizumi *et al.*, 2001; Sassa, unpublished data). High occurrences of *P. piseki* in the stomachs can be explained by the overlap of the nighttime distribution depths of the two species, i.e., more effectively available to *D. fulgens* ascending during the night when the active feeding occurs. In addition, visually oriented predation on bioluminescent prey items, including *Pleuromamma* (Takenaka *et al.*, 2012), has been hypothesized for myctophids (Battaglia *et al.*, 2016). Relatively high %F (32%) of other bioluminescent copepods of *Lucicutia* (Takenaka *et al.*, 2012) in the stomachs of *D. fulgens* also supports this hypothesis.

#### Diel feeding periodicity and daily ration

Migratory myctophids are known to feed actively in the epipelagic layer at night, especially in subtropical and tropical regions where the zooplankton biomass is rather low and restricted in the epipelagic layer (Baird *et al.*, 1975; Clarke, 1978; Kinzer and Schulz, 1985; Dypvik and Kaartvedt, 2013), as they did during the present investigation. *Diaphus fulgens* is considered to occur in the 20–200 m layers at night and in the 400–500 m layers during the daytime (Sassa and Takahashi, 2022). The SCI of *D. fulgens* increased from the early night (1800–2000 h) to the early morning (0400–0800 h), suggesting that they feed actively in the epipelagic layer throughout the night before moving down to the mesopelagic layer. The minimum SCI value was observed from 1600 to



**Figure 5.** Decline in the median stomach content index (SCI) from the early morning (0400–0600 h or 0600–0800 h) to the late afternoon (1600–1800 h). Regression lines (A) from 0500 h (equivalent to 0 h on x-axis of digestion time) to 1700 h and (B) from 0700 h (equivalent to 0 h on x-axis of digestion time) to 1700 h. The instantaneous gastric evacuation rate ( $R$ ) was estimated to be  $0.118 \text{ h}^{-1}$  when fasting starts at the earlier period and  $0.129 \text{ h}^{-1}$  when fasting starts at the later one. Ln SCl, Ln-transformed SCl;  $t$ , digestion time (h).

1800 h, indicating that by this time, digestion and egestion were mostly complete, and little or no feeding occurred during the daytime in the mesopelagic layer. *Diaphus taaningi* captured in the afternoon (1542–1800 h) at 250–270 m had mostly empty digestive tracts (Baird *et al.*, 1975), corresponding with the present study. The present observation suggested that mature individuals of *D. fulgens* maintained a normal diel feeding periodicity during the spawning season.

$R$  has been estimated to be  $0.09\text{--}0.24 \text{ h}^{-1}$  for myctophids in subtropical and tropical waters (Baird *et al.*, 1975; Pakhomov *et al.*, 1996; Williams *et al.*, 2001; Tanaka *et al.*, 2013); thus,  $R$  of *D. fulgens* ( $0.118\text{--}0.129 \text{ h}^{-1}$ ) falls within this range. Estimates of  $R$  are strongly related to habitat temperature (Mendiola *et al.*, 2009; Nikolioudakis *et al.*, 2011). Pakhomov *et al.* (1996) show the relationship between  $R$  and water temperature ( $T$ ) for 20 species of marine planktivorous fishes, including six species of myctophids, from a variety of latitudes with different habitat temperatures, expressed by the power function of  $R = 1/24.3 \times T^{-0.6}$  ( $r^2 = 0.57$ ). In *D. fulgens*, the digestion of food would proceed in the mesopelagic layer between 400 and 600 m, where the water temperature is approximately  $8\text{--}12 \text{ }^\circ\text{C}$  (Sassa and Takahashi, 2022). Substituting  $T$  of  $8\text{--}12 \text{ }^\circ\text{C}$  into the above relationship, the  $R$  of *D. fulgens* was estimated to be  $0.143\text{--}0.183 \text{ h}^{-1}$ , which was approximately 1.1–1.6 times higher than the  $R$  estimated in the present study. When estimating the  $R$  of subtropical and tropical myctophid species using the above relationship, we need to consider the possibility of overestimation of  $R$ .

Based on the estimated  $R$  of  $0.118\text{--}0.129 \text{ h}^{-1}$ , the DR of mature adult *D. fulgens* was calculated to be 4.0–4.2% of BW. Since WW–DW ratios for both mesozooplankton and *D. fulgens* were

approximately 0.20 (Peters and Downing, 1984; Tanaka *et al.*, 2013), the DR on a DW and WW basis would be the same level. The DR of 12 species of migratory adult myctophids in subtropical and tropical waters have been reported to range from 0.8 to 5.7% ( $2.7 \pm 1.5\%$ , mean  $\pm$  SD) of the body DW of the fish (Moku and Hidaka, 2002; Tanaka *et al.*, 2013; Drazen and Sutton, 2017). The DR of *D. fulgens* showed a high value within this range, suggesting active feeding during the spawning season, although a direct comparison of the DR among species should be made carefully due to the difference in the estimation methods among studies (H eroux and Magnan, 1996; Moku and Hidaka, 2002; Drazen and Sutton, 2017) and the difference in SL of fishes analysed (Contreras *et al.*, 2020; Sassa and Takasuka, 2020). Active feeding during the spawning season has also been reported for some other myctophid species (Gartner, 1993; Ishihara and Kubota, 1997; Tanaka *et al.*, 2013; Sassa and Takasuka, 2019).

The daily caloric intake of *D. fulgens* was calculated to be  $21.2\text{--}22.3 \text{ cal day}^{-1}$ . This study assumes that the organic composition of prey items is all protein, although the prey items would also contain lipids with the conversion factors in caloric value of approximately  $8.5 \text{ cal mg}^{-1}$ , i.e., 1.7 times the caloric value of protein (Mayzaud and Martin, 1975; Postel *et al.*, 2000; Harmelin-Vivien *et al.*, 2019). Therefore, the caloric intake would be potentially underestimated, although the percentage of lipids in subtropical and tropical zooplankton is much lower than in Arctic and Antarctic zooplankton species (Harmelin-Vivien *et al.*, 2019). Gartner (1993) estimated the daily caloric intake of a dominant myctophid of *Lepidophanes guentheri* in the eastern Gulf of Mexico to be  $14.8 \text{ cal day}^{-1}$  during the spawning season, which was approximately 0.7 times that of *D. fulgens*.

Generally, multiple spawning fishes, including pelagic and demersal species, largely depend on acquired energy from food during the spawning season for egg production, which has been termed an income breeder (Hunter and Leong, 1981; Witthames *et al.*, 1995; Kjesbu *et al.*, 1998; McBride *et al.*, 2015; Tanaka *et al.*, 2016). The estimated DR showed that *D. fulgens* adults continue to eat food actively during the spawning season, suggesting the characteristics of income breeders. Mei *et al.* (2019) also suggested an income breeder strategy in *D. fulgens* in the Kuroshio waters, based on the similarity between carbon and nitrogen stable isotope ratios measured in larval tissues and those estimated for eggs. *Diaphus fulgens* can be considered to spawn using energy acquired during the spawning season, allocating energy directly to reproduction.

#### Energy balance of multiple batch spawner

High egg production of myctophids, relating to multiple spawning, short interspawn period and high batch fecundity, would contribute to a high abundance of eggs and larvae in the water column (Gartner, 1993; Sassa *et al.*, 2016). This spawning characteristic possibly contributes to the recruitment of sufficient numbers to maintain adult populations. Fat stored in the body would be used for reproduction by myctophid females since the hepatosomatic index (liver weight/BW) and condition factor ( $\text{BW}/\text{SL}^3$ ) are reported to decline during the spawning season in several myctophids (Sassa *et al.*, 2014; Sarmiento-Lezcano *et al.*, 2020). In addition, the present study suggests that acquired energy from food during the spawning season relates to maintaining multiple spawning. In this subsection, to discuss whether females can meet the energetic costs of sustained multiple spawnings by feeding during the spawning season, the caloric expenditure to produce a batch of oocytes was calculated for *D. fulgens* and then compared with daily caloric intake estimated in the present study.



In *D. fulgens*, mean diameter of oocytes after completion of yolk accumulation is reported to be approximately 0.50 mm, median batch fecundity to be 378 eggs (interquartile range: 330–464 eggs), and spawning frequency to be 3–4 days (Sassa and Takahashi, 2022). Assuming the specific gravity of eggs to be 1, the WW of the egg calculated as the volume of a sphere is 0.0654 mg. Thus, the weight of a spawned batch of oocytes is estimated to be 24.72 mg WW ( $=0.0654 \times 378$ ), equivalent to 6.01 mg DW using water content of myctophid ovaries of 75.7% (Gartner, 1993). Caloric content of ovaries is reported to be 1.39 cal  $\text{mg}^{-1}$  WW for the subtropical myctophid *L. guentheri* (Gartner, 1993) and 5.45 cal  $\text{mg}^{-1}$  DW for northern anchovy (*Engraulis mordax*) (Hunter and Leong, 1981). Therefore, the caloric value per spawning batch of *D. fulgens* would approximately range from 32.8 cal ( $=6.01 \times 5.45$ ) to 34.4 cal ( $=24.72 \times 1.39$ ). Based on the spawning frequency of 3–4 days, an energy expenditure ranging from 8.2 cal  $\text{day}^{-1}$  ( $=32.8/4$ ) to 11.5 cal  $\text{day}^{-1}$  ( $=34.4/3$ ) would be needed to produce a batch of oocytes.

In the present study, the daily caloric intake of *D. fulgens* was estimated to be 21.2–22.3 cal  $\text{day}^{-1}$ . Thus, *D. fulgens* can maintain multiple spawnings at a cost of between 36.8% ( $=8.2/22.3 \times 100$ ) and 54.2% ( $=11.5/21.2 \times 100$ ) of the daily caloric intake. The marginal region of the sagittal otolith of mature adult *D. fulgens* collected during February to March has a glass-like structure without clear daily increments (Sassa, unpublished data). Such an otolith structure has been considered to be associated with the stagnation of somatic growth during the spawning season (Katayama, 2018); thus, mature females of *D. fulgens* are considered to invest a larger quantity of energy for the egg maturation process than for somatic growth. Gartner (1993) calculated the energetic costs of sustained multiple spawning with a relatively short interspawn period for *L. guentheri* (approximately 4 days) in the eastern Gulf of Mexico, based on the same procedure to the present study. He suggested that *L. guentheri* maintains multiple spawnings at a cost of approximately 30% of its daily caloric intake. The present estimates for *D. fulgens* were comparable or higher than that of *L. guentheri*. In the future, it is necessary to conduct quantitative examinations of the energetic balance between reproduction and feeding for other species to clarify the reproductive strategy of myctophids.

**Acknowledgements.** We are grateful to the captains, officers and crews of the RV 'Yoko-Maru' and 'Kaiyo-Maru No. 7' and K. Hidaka, S. Kitajima and M. Matsunuma for their assistance in the field. We also thank Y. Hashiguchi of Japan Fisheries Research and Education Agency for helping with the biometric procedure and H. Saito of Suidosha Co. Ltd. for helping with the identification, counting and measuring of prey items.

**Author contributions.** All authors contributed data to the study. C. S. designed and performed the analysis and interpretation of data. C. S. wrote the manuscript with input and revisions from M. T. and Y. T.

**Financial support.** This work was partially supported by the research and assessment programme for fisheries resources, the Fisheries Agency of Japan. This work was supported by grants from the Study of Kuroshio Ecosystem Dynamics for Sustainable Fisheries (SKED) programme of the Ministry of Education, Culture, Sports, Science and Technology of Japan (Grant Number JPMXD0511102330).

**Competing interest.** None.

**Ethical standards.** Not applicable.

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