Title: Respiration rates and active carbon flux of mesopelagic fishes (Family Myctophidae) in the Scotia Sea, Southern Ocean

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Abstract

Mesopelagic fish have recently been highlighted as an important, but poorly studied component of marine ecosystems, particularly regarding their role in the marine pelagic food webs and biogeochemical cycles. Myctophids (Family Myctophidae) are one of the most biomass-dominant groups of mesopelagic fishes, and their large vertical migrations provide means of rapid transfer of carbon to the deep ocean where it can be sequestered for centuries or more. In this study, we develop a simple regression for the respiration rate of myctophid fish using literature-based wet mass and habitat temperature data. We apply this regression to net haul data collected across the Scotia-Weddell sector of the Southern Ocean to estimate respiration rates of the biomass-dominant myctophid species. *Electrona carlsbergi, Electrona antarctica* and *Gymnoscopelus braueri* made a high contribution (up to 85%) to total myctophid respiration. Despite the lower temperatures of the southern Scotia Sea (-1.46 to 0.95 °C), total respiration here was as high (reaching 1.1 mg C m^{-2} d^{-1}) as in the warmer waters of the mid and northern Scotia Sea. The maximum respiratory carbon flux of the vertically migrating community was 0.05-0.28 mg C m^{-2} d^{-1}, equivalent to up to 47% of the gravitational particulate organic carbon flux in some parts of the Scotia-Weddell region. Our study provides the first baseline estimates of respiration rates and carbon flux of myctophids in the Southern Ocean. However, direct measurements of myctophid respiration, and of mesopelagic fish generally, are needed to constrain these estimates further and incorporate these fluxes into carbon budgets.

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Introduction

The biological uptake and cycling of carbon in the ocean are tightly coupled to atmospheric levels of carbon dioxide (CO_2) (Sabine et al. 2004). Primary production in the surface ocean drives the uptake of CO_2, but it only begins to be sequestered once it is transferred below the mixed layer and is no longer in contact with the atmosphere (Primeau 2005). Species that migrate vertically in the water column can actively transfer carbon to the deep ocean through excretion, defecation, mortality and respiration (Longhurst et al. 1990, Zhang & Dam 1997, Steinberg et al. 2000, Turner 2002, Steinberg & Landry 2017, and references therein). This has been studied greatly in marine zooplankton (e.g. Zhang & Dam 1997, Steinberg et al. 2000, Hernández-León et al. 2001, Packard & Gómez 2013), however, there have been few studies examining active transport in migratory fish, particularly mesopelagic fish (e.g. Hidaka et al. 2001; Davison et al. 2013; Hudson et al. 2014; Ariza et al. 2015), which are difficult to sample effectively in remote open ocean regions.

Recently, the importance of including mesopelagic fish in ocean carbon budgets has been highlighted (Anderson et al. 2018). They are one of the components of marine ecosystems that we know least about (St John et al. 2016), yet they are highly motile and many species migrate vertically, feeding at the surface during the night, but migrating to the mesopelagic and bathypelagic zones during the day where they continue to respire. Previous studies have found the respiratory carbon flux of migratory fishes to be equivalent to up to 26% of the gravitational particulate organic carbon (POC) flux (Hidaka et al. 2001, Hudson et al. 2014, Ariza et al. 2015). In addition, their gut passage times are much slower than zooplankton (Ariza et al. 2015), and thus faecal pellets are more likely to be released in the deep ocean following night-time feeding at the surface.

Lantern fish (Family Myctophidae, here after myctophids) are the most common mesopelagic fish in most of the World's oceans (Catul et al. 2011), and are known to make large vertical migrations (Pakhomov et al. 1996). In the mesopelagic and bathypelagic zones of the Southern Ocean, they are the dominant fish family in terms of species richness, abundance, and biomass (Duhamel et al. 2014), and are important in the pelagic ecosystem in this region (Murphy et al. 2007). Yet there have been no studies attempting to quantify the contribution of myctophid species in the Southern Ocean to active carbon fluxes. Indeed, the role of mesopelagic and bathypelagic fish communities in biogeochemical cycling and carbon transfer to depth is one requiring urgent research, both regionally and globally (Trueman et al. 2014).

The respiration rates of myctophid fish are not easy to measure directly, due to difficulties in obtaining live, healthy specimens from the mesopelagic zone, and our inability to successfully incubate them under stress-free conditions. Therefore, previous studies (Hidaka et al. 2001, Hudson et al. 2014) examining myctophid respiration have either utilised the relationship between biomass and respiration established by the historical study of Donnelly and Torres (1988), or used general allometric relationships between mass and metabolic rate for other fish (Davison et al. 2013). An exception is Ariza et al. (2015), who made direct measurements of electron transport system (ETS) activity in order to estimate respiration. A number of large compilations of respiration data have been made, defining regressions between the biomass of marine organisms and their respiration (e.g. Ikeda et al. 2001; Ikeda 2016), yet none of these were specific to myctophid species. There can be significant variation in the resting metabolism, and hence, routine respiration, of different taxonomic groups (Clarke & Johnston 1999). Therefore, generalised regressions for pelagic marine fishes (Ikeda 2016) may not provide the most accurate estimate of myctophid respiration.

In this study, we compile previous estimates of myctophid respiration from the literature to define a simple regression to calculate myctophid respiration from wet mass and habitat temperature. We then utilise net haul data, collected as part of the most comprehensive mesopelagic fish survey in the Southern Ocean to date, to examine myctophid respiration in the Scotia Sea, one of the most productive regions of the Southern Ocean. In this way, we start to quantify their importance in the active transfer of carbon to depth.

Methods

Myctophid distribution and abundance

Detailed surveys for mesopelagic fish were conducted in the Scotia Sea as part of the British Antarctic Survey's Discovery 2010 programme, as has been previously described in Collins et al. (2012). Briefly, this involved deployment of an opening and closing 25 m^2 rectangular mid-water trawl net (RMT25, minimum 4 mm mesh; Piatkowski et al. 1994) along a transect spanning the entire Scotia Sea between the Antarctic Polar Front (APF) and the sea ice zone (SIZ) during three cruises; in November 2006 (cruise JR161, Austral spring), January 2008 (cruise JR177, Austral summer), and March 2009 (cruise JR200, Austral autumn). Depth-stratified net hauls were carried out at six stations that encompassed the main water masses and frontal zones of the region: Polar Front (PF), Southern Scotia Sea (SSS), Mid Scotia Sea (MSS), Western Scotia Sea (WSS), Northern Scotia Sea (NSS), and Georgia Basin (GB). At each station, an RMT25 was deployed at the depth zones: 0-200, 200-400, 400-700, and 700-1000 m. The depth and ambient temperature of the nets were logged using a custom-built net monitoring system. The temperature sensor (SBE-3) was factory calibrated prior to the surveys and was accurate to ~0.001 °C. Net hauls were repeated during the day and night in spring and summer, but only during the night-time in autumn. All fish caught were sorted onboard, identified to the lowest taxonomic level, measured to the nearest mm using standard length (SL) and the wet mass (WM) measured to the nearest 0.01 g using a motion compensated balance. General patterns in community structure of these mesopelagic fish can be found in Collins et al. (2012) and information on species-specific biomass, abundance and population dynamics of the main myctophids is detailed in Saunders et al. (2014, 2015a, b).

For 39% of data records (23, 9, and 97% for JR161, JR177 and JR200 cruises, respectively), the WM was not measured and only the standard length of the fish was recorded. In these instances, we used length-mass regressions from the long-term records held at the British Antarctic Survey (unpubl. data, supplementary Table S1). Where possible, these were species-specific, or else genus-specific for the rarer species. Overall, individual fish WM ranged from 0.03 to 78.34 g (mean 4.38 g).

Myctophid respiration regression

To calculate the total myctophid respiration at each of the sites sampled, we developed a regression based on literature measurements of myctophid respiration. A search of the literature was carried out to identify studies in which the respiration rate of myctophids was measured, and the temperature and body mass (in terms of wet mass (WM), dry mass (DM) or carbon (C)) were also recorded. We identified 5 such studies (Torres et al. 1979, Donnelly & Torres 1988, Torres & Somero 1988, Ikeda 1989, Ariza et al. 2015), giving a total of 74 data points from which we could base our regression analysis (Table 1).

Torres et al. (1979), Donnelly and Torres (1988) and Torres and Somero (1988) measured the routine respiration (i.e. under conditions of normal activity) via incubations at temperatures experienced *in situ*. Both Ikeda (1989) and Ariza et al. (2015) measured the capacity of the respiratory ETS, converting this potential respiration to the actual respiration via experimentally determined ratios. Where possible, we have compiled respiration and WM data for individual fish. However, in instances where the individual-specific data were unavailable, we took either the given mean WM and respiration, or in the case of Torres et al. (1979), the calculated mean WM for the given range.

As the aim was to develop a regression that could readily be applied to fish catch data collected in the field, we chose to develop an equation for the WM specific respiration rate (R_{WM}, in µL O_2 mg WM^{-1} h^{-1}) from fish WM (in mg) and ambient temperature (T, °C). Based on relationships previous established between biomass and respiration (Kiørboe & Hirst 2014, Ikeda 2016), we define a simple regression model.

$$Ln(R_{WM}) = a_0 + a_1 \times Ln(WM) + a_2 \times T \qquad (1)$$

Here a_0, a_1, and a_2 are regression coefficients. Regression analysis was carried out using a regression fitting model for multiple predictors and a response, where data were continuous and no interactions terms were allowed. Wet mass and respiration data were transformed to the natural log prior to fitting the regression. Fitting was performed using the ordinary least squares method in Minitab 18 (version 18.1). To assess the uncertainty surrounding our calculated regression coefficients, we applied bootstrapping. For this procedure, we randomly sampled (with replacement) from all 74 literature-based data points on myctophid fish respiration to generate 100 simulated dataset. We then calculated the regression coefficients (as above) for each of these data sets and in this way, estimated bootstrapped confidence intervals (standard error) for each coefficient over the 100 simulations.

Total respiration

We combine the results of our regression model with the Discovery 2010 survey data to calculate the respiration rate for each individual fish (R_{IND}, µL O_2 ind.$^{-1}$ h^{-1}) in a particular net haul. The total respiration R_{TOT} (µL O_2 m^{-3} h^{-1}) for each net haul was then calculated by standardising to the volume filtered by the net (V, m^3), and summing for all myctophid individuals captured in that haul.

$$R_{TOT} = \sum \frac{R_{IND}}{V} \quad (2)$$

This was then converted to units of carbon per day ($R_{TOT,C}$, mg C m^{-3} d^{-1}) using a respiratory quotient (RQ) of 0.90 for fishes (Brett & Groves 1979, Ariza et al. 2015) and the stoichiometric relationship between carbon and oxygen (22.4 L O_2 = 12 g carbon). For each cruise, at each station, the mean R_{TOT} of any replicate hauls was calculated for each depth horizon. This was computed for day and night hauls separately. Only the night-time data were used for inter-station and inter-species comparisons of total respiration due to the inherent problem of daytime net avoidance by myctophid fish (Pakhomov et al. 1996, Collins et al. 2012) (see below).

Maximum respiratory flux

Many myctophid species are active migrators moving to the euphotic zone at night and returning to depth during the day, fluxing carbon to depth in the process. The maximum respiratory flux (below 200 m) of the migrant myctophid community was calculated by comparing $R_{TOT,C}$ in the 0-200 m depth strata during the day and night (i.e. we subtract the total respiration of the resident community, the day-time respiration (R_d), from the respiration of the night-time community (R_n)). Weather and net failure constraints during the Discovery 2010 cruises resulted in these calculations being possible for four stations, JR161 WSS and NSS, and JR177 MSS and GB. Our respiration calculations for the 0-200 m depth horizon are based on the ambient temperature over this depth range, but migrating individuals will experience different temperatures at depth. Therefore, to estimate the respiration of the migrating community at depth, we recalculated respiration rates using the mean temperature at depths of 400-1000 m. Finally, the maximum daily downward flux of respiratory carbon below 200 m by myctophid migrants (R_m) was estimated based on the number of daylight hours (h) at each station over the period of the research cruise (mean of the maximum and minimum daylight length).

$$R_m = (R_n - R_d) \times \frac{h}{24} \qquad (3)$$

We stress here that these calculations represent the maximum respiratory carbon flux. This is due to the issue of daytime net avoidance (Collins et al. 2012, Fielding et al. 2012). To investigate this uncertainty, we conducted a sensitivity analysis by recalculating day-time respiration assuming catch efficiencies of 14%, 25% and 50%, and used these revised values for sensitivity analysis of the respiratory carbon flux of the migrant myctophid community.

Results

Myctophid respiration regression

The compiled respiration dataset comprised of myctophids (18 species, plus 23 individuals identified to the genus *Myctophum*) of WM ranging from 0.026 – 19.2 g, and experimental temperatures from 0.5 to 27 °C (Figure 1). The respiration rates (mass specific) decrease with increasing WM and increase with increasing temperature (Figure 1).

Regression analysis of the collated data reveals the following regression for mass specific respiration (R_{WM}) of myctophid fishes (n=74, adjusted R^2=0.85), with standard error of coefficients shown in brackets:

$$Ln(R_{WM}) = -1.315\ (\pm 0.468) - 0.2665\ (\pm 0.0516) \times Ln(WM) + 0.0848\ (\pm 0.0108) \times T \qquad (4)$$

The standard errors calculated from our bootstrap analysis were 0.0368, 0.0040 and 0.0010 for a_0, a_1, and a_2 respectively. R_{WM} increases with increasing temperatures (supplementary Figure S1) and decreases with increasing wet mass (supplementary Figure S2).

Myctophid respiration: Seasonal changes

Total respiration was calculated for each haul of the Discovery 2010 cruises, highlighting both latitudinal and seasonal patterns. We present the seasonal change in total myctophid respiration for the NSS, MSS and SSS stations (Figure 2) as these are the stations where we have data from all four depth horizons on all three cruises. Night-time only data is examined to avoid bias by net avoidance during the day. Total respiration (integrated from 0-1000 m depth) was highest at SSS in autumn (1.0 mg C m^{-2} d^{-1}), with the lowest rates occurring at NSS in autumn (0.4 mg C m^{-2} d^{-1}). Whereas total respiration increased from spring to autumn at SSS, the opposite pattern was observed at NSS. Total respiration peaked at 1.0 mg C m^{-2} d^{-1} in summer at MSS.

Seasonal differences were also apparent in the species making the dominant contribution to the total respiration (Figures 3-5). At NSS (Figure 3), *Electrona carlsbergi* accounted for 51% of the total respiration in spring. As the season progressed at NSS, the total respiration decreased for all species except *Electrona antarctica*, which peaked in summer, and the contribution to total respiration was much more equal across the different species.

At MSS (Figure 4), the highest total respiration was also due to *E. carlsbergi* but, in this case, this occurred in the summer, contributing 43% to the total respiration. *E. antarctica* also made a strong contribution (26%) to total respiration at MSS in summer. In both the spring and autumn, *Gymnoscopelus braueri* dominated the total respiration (38 and 33% respectively). At SSS (Figure 5), *E. antarctica* and *G. braueri* were the dominant species in terms of total respiration, with *G. braueri* dominating in spring (39%) and *E. antarctica* dominating in summer (47%) and autumn (45%).

Myctophid respiration: depth stratified, day – night comparisons

There are four sites where we have complete day and night data for all four depth horizons (Figure 6), WSS and NSS in the spring, and GB and MSS in the summer. Total respiration was highest at night-time, possibly because this was when more fish were caught, however, the potential net avoidance during the day makes it difficult to ascertain exact migration patterns. In the summer, *E. antarctica* dominated the total depth integrated respiration during both the day and night at MSS, however, during the day, respiration was highest in the 0-200 and 401-700 m depth horizons (0.0007 and 0.0006 mg C m^{-3} d^{-1} respectively) whereas, at night, respiration of *E. antarctica* was highest (0.0009 mg C m^{-3} d^{-1}) in the 701-1000 m depth range. Generally there was a decline in the total respiration with depth during the night, and an increase with depth during the day.

Although a particular species may dominate the total depth integrated respiration, this may be confined to particular depth horizons (Figure 6). For example, *E. carlsbergi* appears to contribute markedly to the total respiration at NSS in spring and MSS in summer (Figure 6), but our data suggest that its contribution is limited to the upper 400 m of the water column. Conversely, in the summer, both *E. antarctica* and *G. braueri* were important contributors to the myctophid respiration at all depth horizons during the day and night, with possible net avoidance or migration out of the top 200 m during the day.

Maximum respiratory flux

Of the four sites where data were sufficient, the maximum respiratory flux of carbon below 200 m by the migrant myctophid community was highest at NSS in the spring (0.28 mg C m^{-2} d^{-1}). The maximum respiratory carbon flux at GB in summer was lower (0.13 mg C m^{-2} d^{-1}), with the lowest flux of 0.05 mg C m^{-2} d^{-1} at WSS in spring.

As net sampling of nekton is not 100% efficient, with net avoidance being a particular problem during the daytime, we conducted a sensitivity analysis to examine how this alters our calculations of the respiratory carbon flux. Studies have found net capture efficiencies of ~14% for net mouth areas between 5 and 105 m^2 (Koslow et al. 1997, Davison 2011). We take this as a lower bound estimate for our sensitivity analysis, recalculating the respiratory carbon flux based on day-time capture efficiencies of 14, 25, and 50% (Table 3).

Our sensitivity analysis highlights that these uncertainties in catch efficiency present problems for accurately incorporating these fluxes into mesopelagic carbon budgets. In two instances (JR161 WSS and JR177 GB), the respiratory flux assuming 14% day-time capture efficiency results in slightly negative estimates of respiratory carbon flux. However, it is also likely that there is also some net avoidance at night-time which we have not attempted to account for here due to unknown catch efficiencies.

Discussion

Catch efficiency

Considering the lack of data on mesopelagic fish respiration, and difficulty of obtaining such data, we attempt here to estimate respiration of the dominant fish, myctophids, in the Southern Ocean, based on biomass and temperature data. In this way we can start to assess the importance of mesopelagic fish in the Southern Ocean carbon budget. Although our calculations are based on a dedicated survey programme, spanning multiple regions and seasons, the biomass data are from net hauls and hence suffer the problems of net avoidance and catch efficiency.

The sampling of fish, and miconekton generally, via nets is fraught with the loss of individuals due to both net avoidance by large, fast swimmers during the day, and the loss of smaller animals through the mesh of the net. The capture efficiency is related to the net design as well as to the size and swimming ability of micronekton (Gartner et al. 1989, Itaya et al. 2007), it is therefore not possible to apply a single correction factor. Acoustic estimates of biomass are generally greater than those from net trawls (e.g. Koslow et al. 1997; Kaartvedt et al. 2012; Davison et al. 2015a), but acoustic estimates of mesopelagic fish biomass also present several challenges and require thorough ground-truthing (Davison, Koslow, et al. 2015). The sensitivity analysis that we conducted (Table 3) increases the range of our estimates of respiratory active flux, highlighting the need for new developments in acoustic techniques to improve myctophid abundance estimation that will further constrain estimates of respiratory flux by mesopelagic fish.

Myctophid respiration regression

Analysis of the myctophid data we collated shows the expected trends of increasing mass specific respiration with increasing temperature and, decreasing mass specific respiration with increasing WM, as have been found by previous respiration studies (Winberg 1956, Clarke & Johnston 1999, Ikeda 2016). The aim of this study is not to examine the theory behind the success of various predictors, but to develop a simple equation to make first order estimates of the respiration of myctophid fishes. Our regression therefore uses parameters that are easily measurable in the field, T and WM.

Although our respiration regression is predominantly driven by abundance and WM, we do not see the same patterns for respiration as have been shown for abundance for the Discovery 2010 data. The calculated respiration depends on not only the total biomass, but also on the contribution of different sized fishes to the total biomass. For example, we would calculate much higher mass specific respiration (and lower total respiration) for a site with large numbers of small sized individuals, compared to a site with the same biomass but comprised of fewer numbers of larger individuals. As the *in situ* temperature of the data used from the Discovery 2010 cruises had a small range of -1.46 – 3.31 °C (based on mean net haul temperatures), temperature plays a smaller role in the differences in respiration between stations.

The regression we have developed is based on a relatively small number of studies (*n*=5) and data points (*n*=74), each of which is associated with methodological weaknesses. Torres et al. (1979), Donnelly and Torres (1988) and Torres and Somero (1988) conducted incubations on live fish to measure respiration. These incubation-based measurements can introduce errors due to stress during net capture and incubation, starvation and bacterial growth. This is particularly true in highly motile myctophid fish that migrate in the water column. Although the ETS method adopted by Ikeda (1989) and Ariza et al. (2015) avoids these issues by measuring the capacity of the respiratory ETS on frozen specimens, there are uncertainties in the choice of ratio to convert from potential respiration to actual respiration. The inclusion of data collected via both of these methods reduces the influence of any methodological bias on our results. Additionally, we conduct a bootstrap analysis to assess uncertainties in our regression model. Although the standard errors calculated for each coefficient (used to define error bars in Figure 2) were relatively small, they do not take into account uncertainties in biomass. It is a major challenge, to sample these mesopelagic fish repeatedly at such a spatial scale, and thus although we are unable to quantify uncertainties surrounding total biomass estimates at each station, we believe our analysis is a useful step forward in a complex and poorly-studied area.

To allow comparison to studies compiling larger data sets of fish metabolism, we reran our regression model using the same data but with respiration rates in units of µL O_2 Ind.$^{-1}$ h^{-1}

(R_{IND}), rather than mass specific respiration. This allows us to calculate the mass scaling coefficient (a_1) to compare with other studies.

$$Ln(R_{IND}) = a_0 + a_1 \times Ln(WM) + a_2 \times T \quad (5)$$

This reveals a mass scaling coefficient of 0.734 (0.682-0.785), comparing well to the coefficients found by Ikeda (2016) (0.843-0.925), Clarke and Johnston (1999) (0.79-0.83) and Winberg (1956) (0.687-0.930). This gives confidence that the myctophid respiration dataset is sufficient to capture relationships between respiration, mass and temperature. Our compiled data set covers several orders of magnitude in WM (0.026 – 19.2 g), and a wide temperature range from 0.5 to 27 °C. However, these studies in themselves are subject to limitations as discussed above.

Although relations between mass and metabolic rate have been found when examining organisms over many orders of magnitude in size (Brown et al. 2004), there is much scatter around this relationship. A review by Seibel and Drazen (2007) highlighted a 300-fold variation in metabolic rates between the fastest and slowest marine animals that was independent of body mass and temperature. Potential differences in locomotory capacity between the myctophid species used to develop our regression model and those sampled in our study region therefore adds to the uncertainty in our calculated respiration rates.

Species contribution to total respiration

We find that, for the three sites analysed here, NSS, MSS, and SSS, *Electrona carlsbergi, Electrona antarctica* and *Gymnoscopelus braueri* were the dominant contributors to respiration. These species were also dominant in terms of total biomass (Collins et al. 2012, Saunders et al. 2014, 2015a) highlighting that, of the terms in our regression model, total biomass is a more important determinant of community respiration than individual fish mass or temperature when considering the Scotia Sea as a whole. This is likely because the range in temperatures across our study site is small (-1.46 – 3.31 °C). However, the differences in species composition regionally within the Scotia Sea likely contributes to the regional differences we see in total respiration (Figure 2).

Collins et al. (2012) noted a higher species diversity in the northern Scotia Sea where temperatures are warmer. This is likely related to the need to attain a greater body size at the colder temperatures of the southern Scotia Sea, hence preventing smaller species and intra-specific life stages from penetrating the southernmost regions (Saunders & Tarling 2018). Similar macroecological trends in diversity and body size have also been reported for fish communities globally (Fisher et al. 2010a, b). *G. braueri* and *E. antarctica* were the dominant species in terms of abundance in the southern Scotia Sea, whereas *E. carlsbergi*, *Krefftichthys anderssoni* and *Protomyctophum bolini* were dominant in the northern stations (Saunders et al. 2014, 2015a, b). The size of *G. braueri* and *E. antarctica* (34-162 mm and 24-115 mm SL respectively) is larger than that of *E. carlsbergi*, *K. anderssoni* and *P. bolini* (68-90 mm, 15-74 mm and 23-66 mm SL respectively), which may in part explain why total respiration rates in the SSS were typically higher than those in the NSS.

Additionally, as species-specific respiration rates are calculated from a general regression for myctophids, if there are large inter-species variations in respiration (e.g. due to differences in locomotory capacity, diet and behaviour etc), it is possible that less abundant species could make greater contributions to total respiration than we have estimated here. However, there are currently insufficient data to develop species-specific mass-respiration relationships. It is difficult to collect healthy, live fish from mesopelagic depths for use in incubation experiments, and *in situ* incubations at depth are not yet feasible for the majority of scientific research cruises. We suggest that estimating respiration through the measurement of ETS activity (Packard & Christensen 2004, Ariza et al. 2015) provides a good alternative, particularly in revealing interspecific differences.

Seasonal patterns in total respiration

Comparison of integrated respiration at NSS, MSS, and SSS (Figure 2) highlights strong seasonality in the NSS compared to MSS and SSS. As *E. carlsbergi*, a predominantly copepod feeding species(Saunders et al. 2015a), accounted for most of the biomass and myctophid respiration at the NSS site in spring, it is possible that high respiration here was driven by the large phytoplankton blooms (Korb et al. 2008, 2012) and high mesozooplankton abundances (Ward et al. 2012) that occur in the region. It has been suggested that *E. carlsbergi* may be associated with warm water eddies from the Polar Front (Collins et al. 2012) which, if more prevalent in spring, could explain the seasonal decline in the contribution of *E. carlsbergi* to myctophid respiration at NSS. The dominance of *E. carlsbergi* to total respiration at NSS in spring highlights that migration behaviour and oceanic transport mechanism from more remote regions can be an important factor in community respiration in the Southern Ocean.

Whereas total respiration was greatest in spring at NSS, the maximum respiration occurred in summer and autumn at MSS and SSS respectively. The spring peak at NSS may be related to the aforementioned migration patterns of *E. carlsbergi.* The later peak in myctophid respiration in the southern Scotia Sea may be linked to ice cover, with the timing of ice retreat influencing the development of zooplankton (Korb et al. 2012), which are the prey for the myctophid species at our study site (Saunders et al. 2014, 2015a). During the same Discovery 2010 cruises, Ward et al. (2012) observed highest zooplankton abundances in the autumn in the southern Scotia Sea.

It is very interesting that, despite the low temperatures of the SSS station (-1.46 to 0.95 °C, based on mean net temperatures), total respiration rates are still high and comparable to both MSS and NSS where temperatures are higher (Figure 2). Thus, despite much higher zooplankton abundances in the NSS, in terms of myctophid respiration, total respiration is actually higher in the SSS. The higher abundance of myctophids in the SSS likely explains these regional patterns in total respiration, with higher abundances perhaps relating to food availability, or to the refuge from predation that the sea ice zone provides. Krill abundances are high across the Scotia Sea (Atkinson et al. 2008), but more krill are found in the southern Scotia Sea (Fielding et al. 2012) where most spawning occurs (Murphy et al. 2007). Therefore, higher abundances of krill in the sea ice zone, particularly of smaller life stages that fall more within the prey size spectra for myctophids may explain, at least in part, the higher abundances of some myctophid species in the southern Scotia Sea.

Since there are regional differences in prey availability, and myctophids can select larger, more energy rich copepodite stages when feeding (Shreeve et al. 2009), prey quality may also play a role in the regional patterns in total respiration. Additionally, as krill typically have a higher energetic density than copepods (Schaafsma et al. 2018), the increase in krill predation by *E. antarctica* with increasing latitude southwards (Saunders et al. 2014) could support higher metabolic activities and contribute to higher total respiration at SSS. However, as our respiration estimates are based primarily on patterns of myctophid abundance, it would be useful to validate our finding of higher respiration rates in the SSS by direct measurements of respiration at these sites. If abundance is indeed the primary driver, then the high spatio-temporal variability in myctophid distribution and abundance (Collins et al. 2012) has important consequences for active carbon fluxes in the Scotia Sea.

Respiratory carbon flux

We calculate a maximum respiratory carbon flux of 0.05-0.28 mg C m^{-2} d^{-1} based on net catch data that has not been corrected for catch efficiency. This is at the low end of previous estimates of myctophid/micronekton respiration (Table 2) even when rates are adjusted for differences in *in situ* temperatures. Individual fish WM ranged from 0.03 to 78.34 g (mean 4.38 g) compared to 0.085 to 0.225 g (mean 0.163 g) in the study of Ariza et al. (2015). As respiration rates are higher for larger individuals, it is surprising that respiratory carbon fluxes calculated by Ariza et al. (2015) are so high, considering the community of small sized fish in their study. Size is therefore not the only important factor to consider, and differences in the locomotory capacity and behaviour of the fish species in the various studies could also contribute to differences in respiratory carbon fluxes. Hidaka et al. (2001) and Hudson et al. (2014) do not give individual fish weights to allow size based comparisons. The different methods of sampling and calculation of respiratory flux in the aforementioned studies make direct comparisons difficult, but it is clear that our estimates sit in the range of previous estimates.

To assess the potential importance of the respiratory carbon flux of myctophid fishes in the Scotia Sea we compare our data to the gravitational flux of POC at two sediment traps, P2 at

1500 m (at NSS site) and P3 at 2000 m (at GB site) (Manno et al. 2015). Between 2008 and 2010, POC fluxes in November at P2 ranged from 0.6 to 3.2 mg C m^{-2} d^{-1}, and from 7.1 to 13.1 mg C m^{-2} d^{-1} at P3 in January (Manno et al. 2015). These compare to a maximum respiratory carbon flux of 0.28 mg C m^{-2} d^{-1} at NSS and 0.13 mg C m^{-2} d^{-1} at GB respectively. The myctophid respiratory carbon flux alone (i.e. excluding other myctophid driven carbon fluxes via excretion, mortality and defaecation) is equivalent to 9-47% and 1-2% of the gravitational POC flux at NSS and GB respectively. These are higher than Hidaka et al. (2001) and Ariza et al. (2015) measured for euphausiids and decapods in the Canary Islands and western Equatorial Pacific (euphausiid and decapod respiration were equivalent to up to 1.6% and 1.4% of total POC flux respectively). For comparison, data compiled by Steinberg & Landry (2017) shows that the respiratory fluxes of zooplankton are typically higher (up to ~30 mg C m^{-2} d^{-1}) than our estimates for myctophid fish. However, differences in biomass, temperature and depth, for example, make it hard to compare values directly. Their study further revealed a positive trend between percent contribution to POC and respiratory flux, with zooplankton respiratory fluxes < 2 mg C m^{-2} d^{-1} corresponding to a contribution to POC flux of <15%. Despite relatively low total respiratory fluxes in comparison to zooplankton, our data suggest that the percent contribution can still be high for myctophids.

Although our estimate of respiratory carbon flux is a maximum, due to possible day-time net avoidance, actual active rates of respiration will be higher than the routine respiration rates calculated here, once physiological processes, such as feeding, swimming activity and reproductive development have been accounted for. The relationship between the active metabolic rate (the highest rate of energy expenditure) and the basal or standard metabolic rate (the minimum energy expenditure required to keep the fish alive) can be as high as 14

(Steffensen, John 2005). Johnston et al. (1991) measured the oxygen consumption of the Antarctic teleost fish, *Notothenia neglecta*, finding that active consumption rates were 4-7 times higher than resting rates. The prior feeding conditions, diet and activity level all affect respiration, and organisms can adjust their rates of respiration in response to variations in food supply (Brown et al. 2004). It is therefore not possible to explain all the variation in respiration rates with T and WM alone, and *in situ* rates of active respiration will be higher than the routine respiration rates estimated here.

Fish also contribute to carbon export via mortality, excretion (dissolved organic carbon) and the production of faecal pellets, such that the total contribution of myctophids to the transfer of carbon to depth will be greater than we have estimated here. We also estimate the gut flux, i.e. the flux of POC in faceal pellets containing non-assimilated food. The energy budgets of Brett and Groves (1979) give a value of 40% for the percentage of respired carbon that is defecated. The proportion of defecated carbon that is produced in the deep ocean will depend on the gut clearance time and duration spent at depth. We conservatively assume that half of the defecation (i.e. 20% of the respiratory flux based on Brett and Groves (1979)) occurs at depth, and calculate gut fluxes of 0.01-0.06 mg C m^{-2} d^{-1} for the migrating myctophids at our case study sites. This increases the active flux to 0.06-0.34 mg C m^{-2} d^{-1} (total respiratory and gut flux). At NSS and GB, this equates to 10.5-56.0% and 1.2-2.1% of the gravitational POC flux at NSS and GB respectively. Myctophid fishes can therefore be an important component of the mesopelagic carbon budget, particularly considering the vertical migrations they undertake (Pakhomov et al. 1996).

Concluding remarks

Our analysis of the literature on myctophid respiration rates, and its application to the Discovery 2010 survey data, reveals that myctophid respiration could indeed make a significant contribution to fluxes of carbon to the deep ocean in the Scotia Sea. Our estimates are based on allometric equations and could be improved through the further integration of direct, species-specific measurements of myctophid respiration. There is also a need to assess daytime avoidance, for instance, through comparison with acoustic observations. Given the extent of their potential contribution, it is now key that future work further constrains the levels of carbon flux generated by myctophid fish so that they may be appropriately included in global biogeochemical models.

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Data Availability

The fish length and weight data utilised in this study can be accessed at the following DOI: XXXXXXXX

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Tables

Table 1: Data sources for respiration rates of myctophid species

Reference	Location	Myctophid species	Experimental Temperature (°C)	Wet mass range (g)	Range in species maximum length (cm) ^
Donnelly & Torres (1988)	Eastern Gulf of Mexico	*Diaphus mollis, Lampanyctus nobilis, Lepidophanes guentheri, Myctophum affine*	7-20	0.112-6.155	6.6-12.4
Torres et al. (1979)	Southern California	*Diaphus theta, Lampanyctus regalis, Lampanyctus ritteri, Parvilux ingens, Stenobrachius leucopsaurus, Symbolophorus californiensis, Tarletonbeania crenularis, Triphoturus mexicanus*	5-13	0.9-13.7	7.0-21.0
Torres & Somero (1988)	Antarctica	*Electrona antarctica, Gymnoscopelus braueri, Gymnoscopelus opisthopterus*	0.5	1.0-40.0	11.5-16.2
Ariza et al. (2015)	Canary Islands	*Lobianchia dofleini*	17.5-19	0.085-0.225	5.0
Ikeda (1989)	Coral Sea, South Pacific	*Symbolophorus evermanni, Centrobranchus nigroocellatus, Myctophum spp.*	24-27	0.026-1.101	5.0-8.0

^ Maximum lengths (SL, with the exception of species in the study of Torres et al. 1979 which are total length) of each species have been obtained from Fish Base (Froese & Pauly 2018), and we present here the range in these lengths for the species within each study.

Table 2: Comparison of respiratory carbon fluxes (mg C m^{-2} d^{-1}) calculated in this study, and in the literature.

Reference	Location	Site	Taxa	Migrant biomass (mg C m^{-2})	Temperature at depth (°C)^	Respiratory Flux * (mg C m^{-2} d^{-1})	Respiratory Flux at 2 °C ** (mg C m^{-2} d^{-1})
This study [a]	Southern Ocean	JR161 WSS	Myctophidae	49.8	2.0	0.05 [+]	0.05 [+]
		JR161 NSS		520.6	2.1	0.28 [+]	0.28 [+]
		JR177 GB		238.5	1.7	0.13 [+]	0.13 [+]
		JR177 MSS		407.1	0.7	0.27 [+]	0.33 [+]
Ariza et al. (2015)[b]	Canary Islands	Time-series station (north of Gran Canaria)	Migratory fish	168	12	2.68	0.69
			Migratory nekton [c]	201	12	2.92	0.7
Hudson et al. (2014)[a]	North Azores	Reykjanes Ridge	Migratory Myctophidae	5.2	6.6	0.005-0.027	0.003-0.014
		Azorean Zone		40	11.8	0.046-0.271	0.012-0.071
Hidaka et al. (2001)[a]	Western equatorial pacific	Station 15	Migratory Myctophidae	462.5	9.3	1.98	0.73
		Station 16		248.9	9.3	1.06	0.39
		Station 8	Night-time Myctophidae	539.5	9.3	2.31	0.86
		Station 10		406.5	9.3	1.74	0.64
		Station 13		716.92	9.3	3.07	1.1

^ Temperature depth ranges as follows: This study: mean 400-1000 m, Ariza et al. (2015): approximate temperature 400-500m, Hudson et al. (2014): mean 200-750 m, Hidaka et al. (2001): 400 m

*Flux below following depths: This study: 200 m, Ariza et al. (2015): 150 m, Hudson et al. (2014): 200 m, Hidaka et al. (2001): 160 m.

** Adjusted to 2°C based on a Q10 of 3.9 for myctophids (Donnelly & Torres 1988)

[+] Maximum respiratory carbon flux as day-time net catches have not been corrected for capture efficiency

[a] uncorrected for capture efficiency

[b] assumes 14% capture efficiency

[c] fish, euphausiids and decapods

Table 3: Sensitivity analysis of respiratory carbon flux estimates. Flux estimates have been recalculated based on day-time net capture efficiencies of 14%, 25% and 50%.

Site	Respiratory flux (mg C m^{-2} d^{-1})			
	100%	14%	25%	50%
JR161 WSS	0.05	-0.00	0.02	0.04
JR161 NSS	0.28	0.24	0.26	0.27
JR177 GB	0.13	-0.00	0.06	0.11
JR177 MSS	0.27	0.25	0.26	0.27

Figures

A)

B)

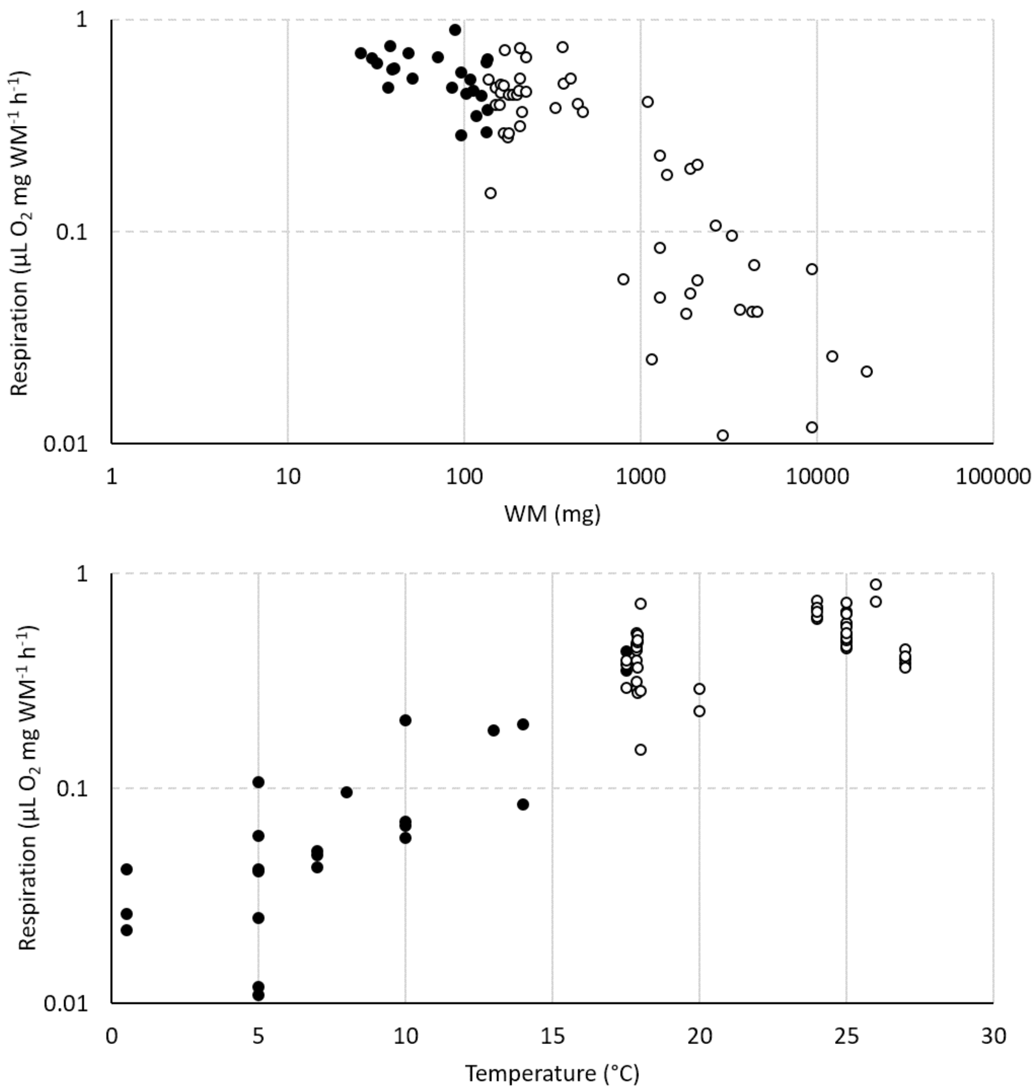

Figure 1: Literature compilation of respiration rates (mass specific) of myctophid fishes versus A) wet mass (WM), and B) temperature. Note the logarithmic scales. Filled black circles show data from direct oxygen consumption experiments, and open circles show respiration estimated from ETS measurements.

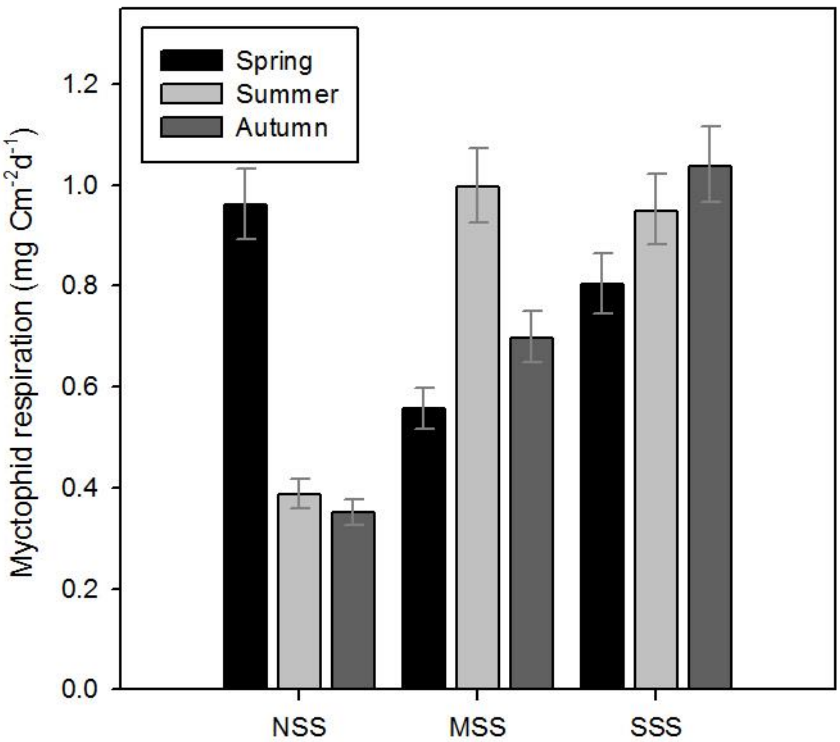

Figure 2: Seasonal changes in total myctophid respiration (mg C m^{-2} d^{-1}, depth integrated 0-1000 m) in the North Scotia Sea (NSS), Mid Scotia Sea (MSS) and South Scotia Sea (SSS). Data are from night-time hauls only. Error bars display the standard error of bootstrapping analysis (100 runs) of our length-mass regression only (see Methods for full details).

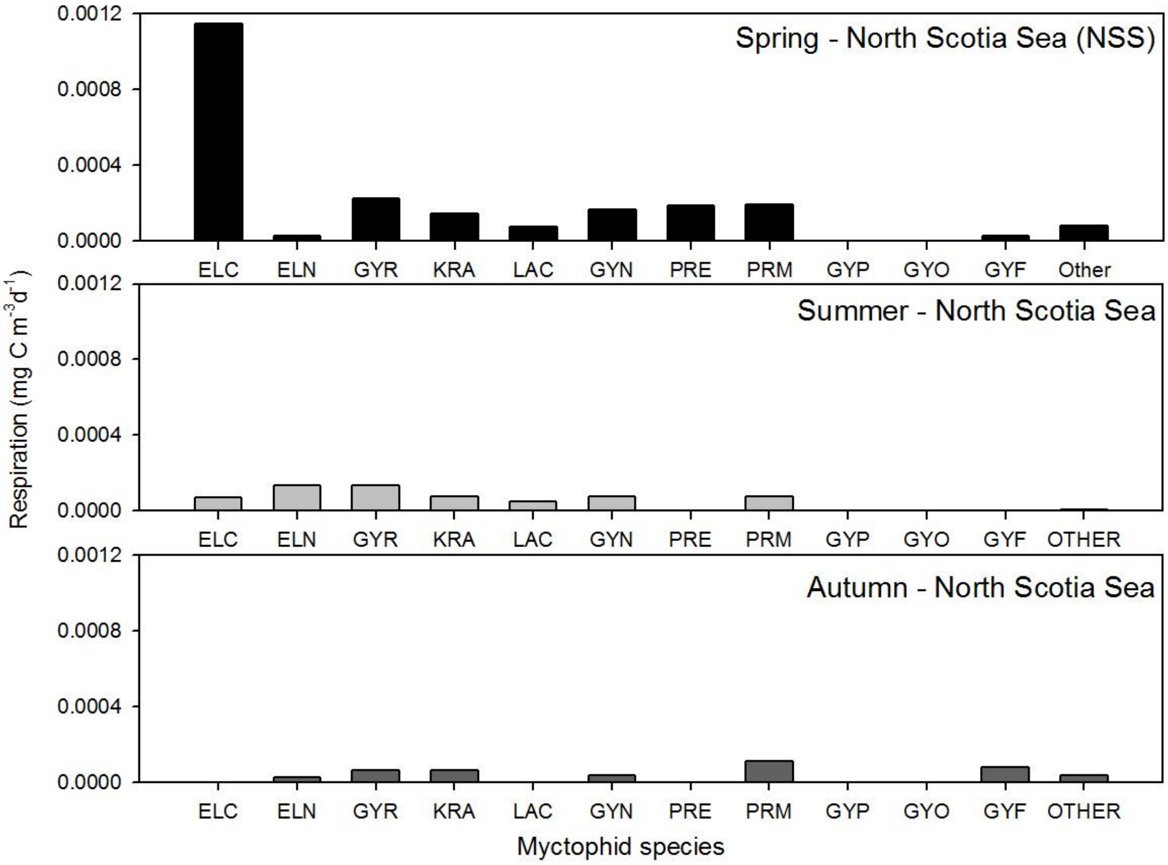

Figure 3: Seasonal change in total respiration (mg C m^{-3} d^{-1}) of myctophid fishes caught in the upper 1000 m at the North Scotia Sea (NSS) station. Species code names are as follows: ELC= *Electrona carlsbergi*, ELN = *Electrona antarctica*, GYR= *Gymnoscopelus braueri*¸ KRA= *Krefftichthys anderssoni*, LAC= *Nannobrachium achirus*, GYN= *Gymnoscopelus nicholsi*, PRE= *Protomyctophum tenisoni*, PRM= *Protomyctophum bolini*, GYP= *Gymnoscopelus piabilis*, GYO= *Gymnoscopelus opisthopterus*, GYF= *Gymnoscopelus fraseri*, OTHER= Other myctophid species. Data from night-time hauls only. Zero values represent species absence.

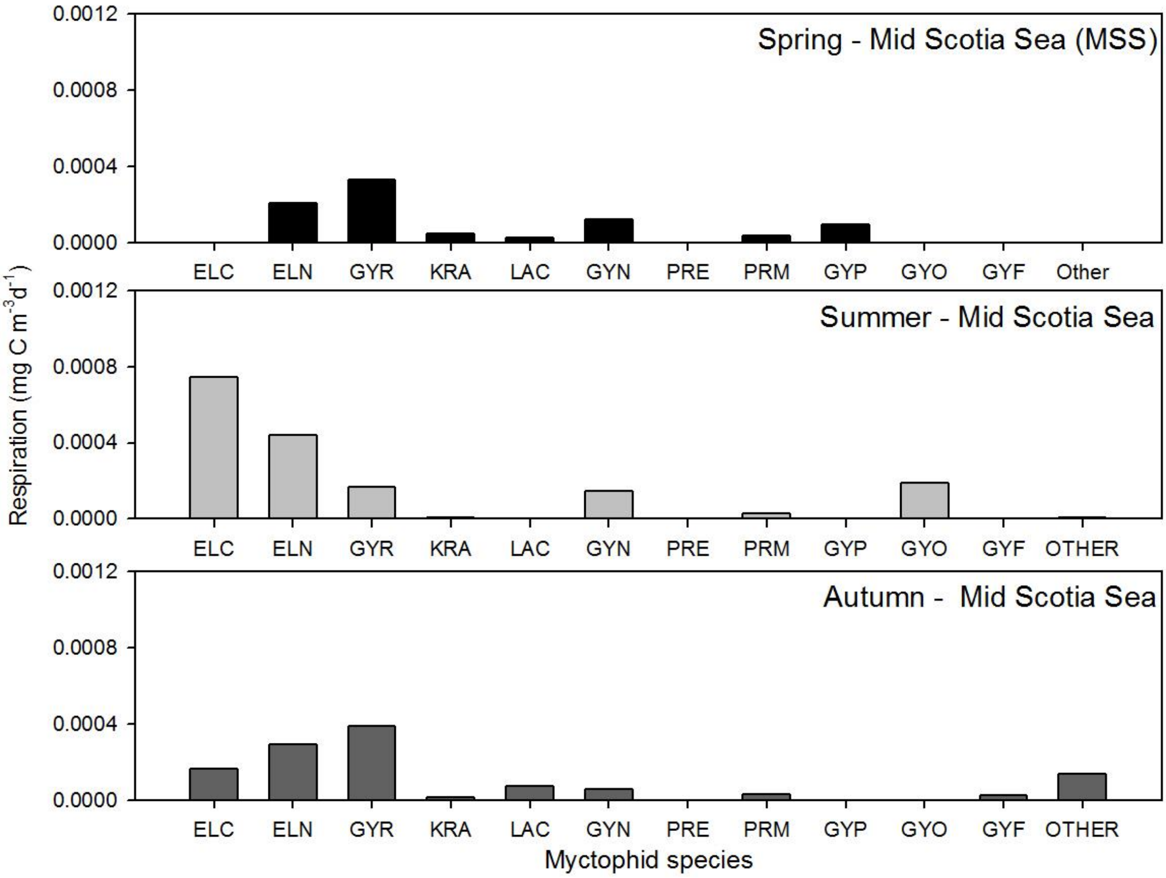

Figure 4: Seasonal change in total respiration (mg C m^{-3} d^{-1}) of myctophid fishes caught in the upper 1000 m at the Mid Scotia Sea (MSS) station. Species code names are as of Figure 3. Data from night-time hauls only. Zero values represent species absence.

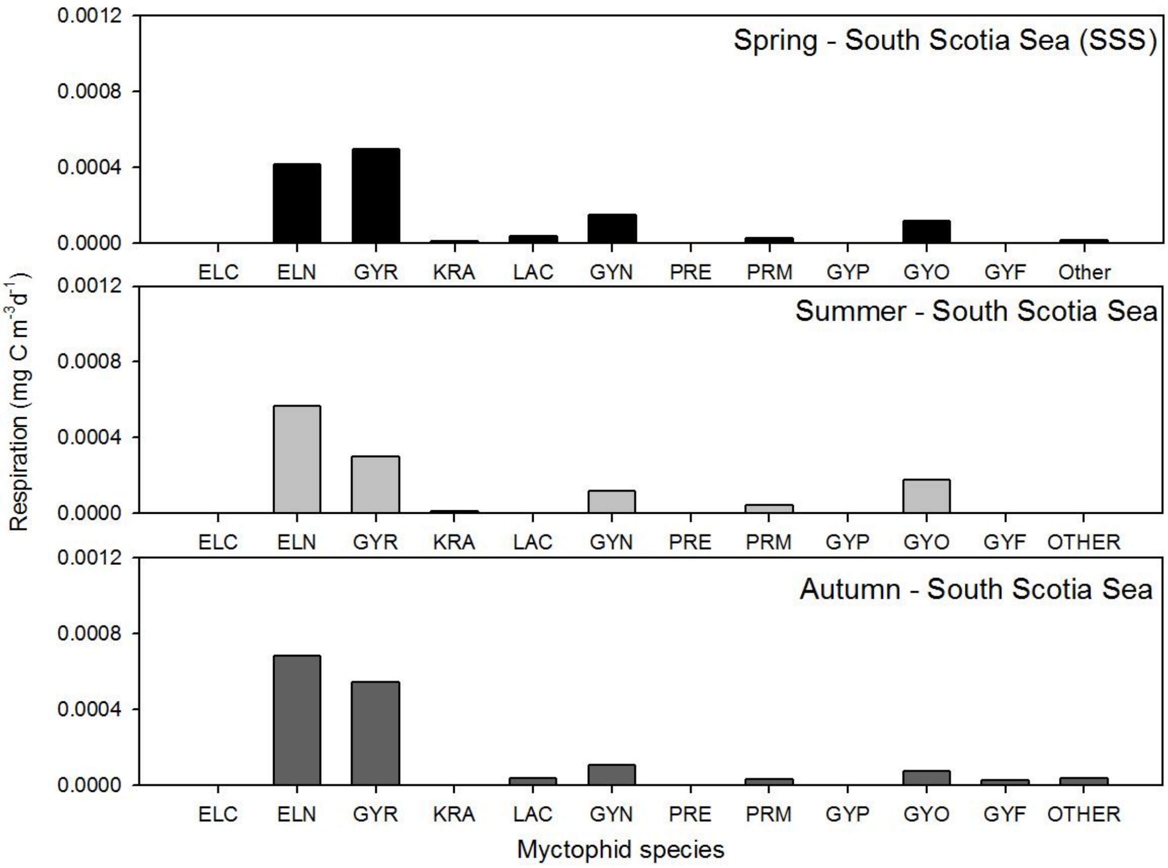

Figure 5: Seasonal change in total respiration (mg C m^{-3} d^{-1}) of myctophid fishes caught in the upper 1000 m at the South Scotia Sea (SSS) station. Species code names are as of Figure 3. Data from night-time hauls only. Zero values represent species absence.

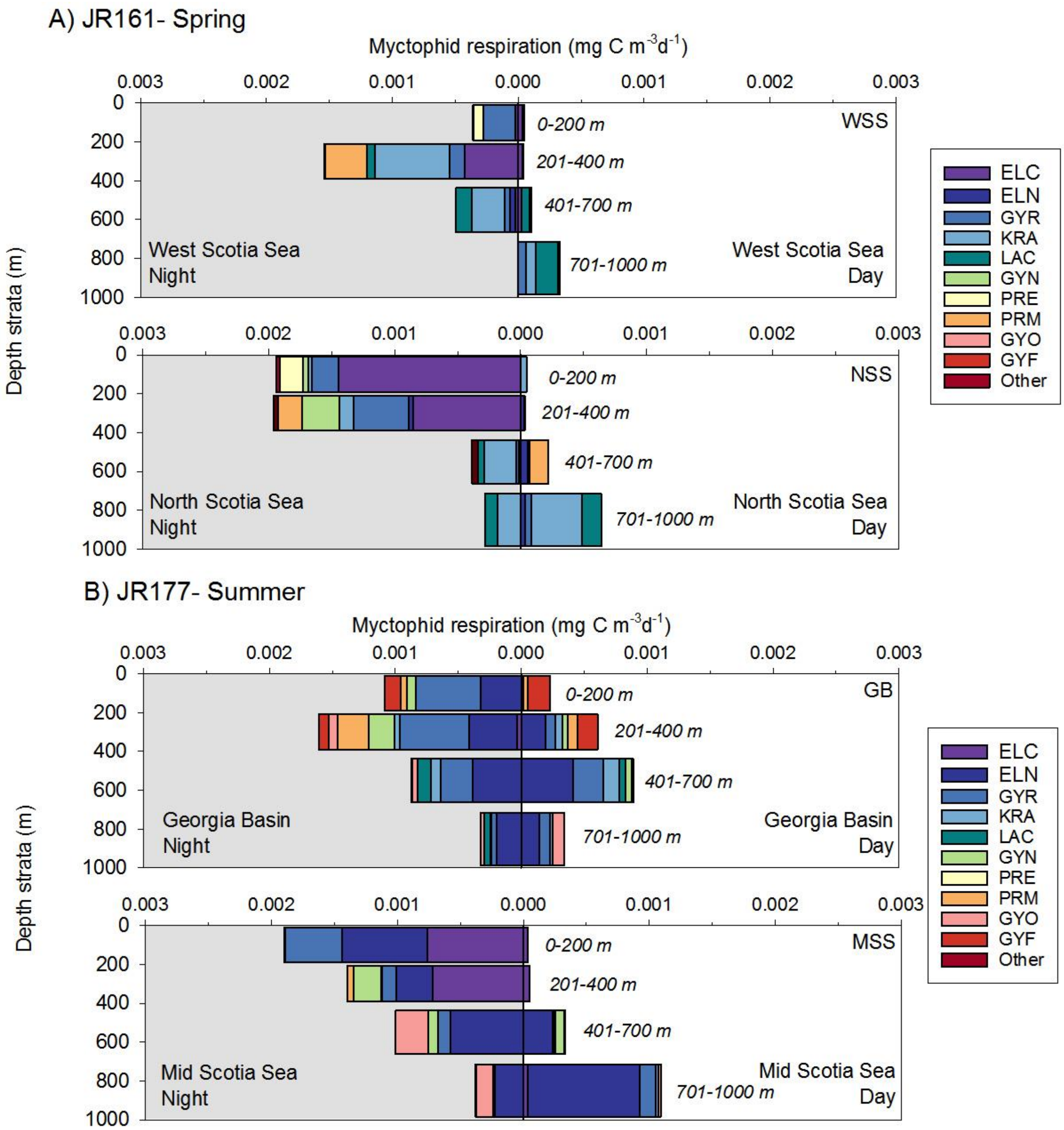

Figure 6: Contribution of the dominant myctophid species to the depth stratified respiration in A) spring – cruise JR161 and B) summer – cruise JR177. Total respiration (mg C m^{-3} d^{-1}) for each species has been calculated for both the day and night (grey shaded graph) net hauls. Species code names are as of Figure 3.

Supplementary Material

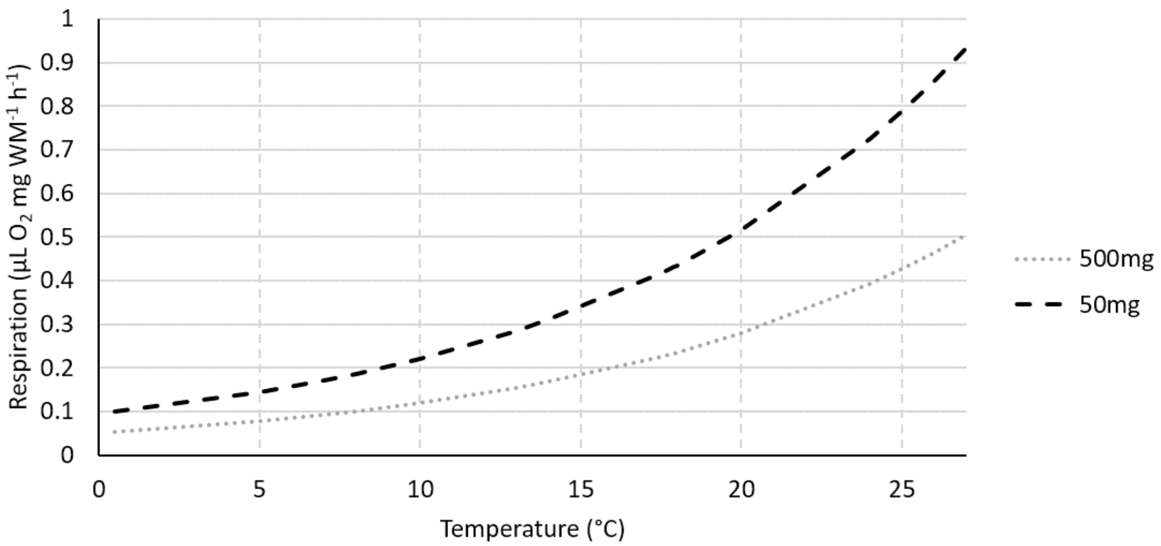

Figure S1: Calculated relationship between temperature (°C) and mass specific respiration rate (µL O_2 mg WM^{-1} h^{-1}) for myctophid fishes of wet mass 50 mg (black dashed line), and 500 mg (grey dotted line).

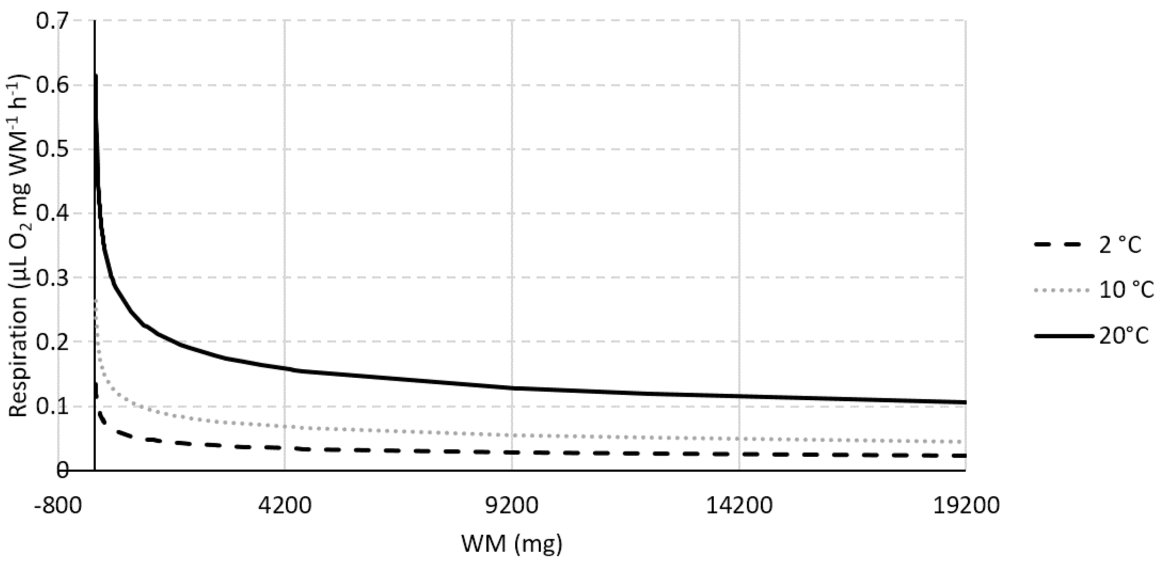

Figure S2: Calculated relationship between temperature (°C) and mass specific respiration rate (µL O_2 mg WM^{-1} h^{-1}) for myctophid fishes at temperatures of 2 °C (black dashed line), 10 °C (grey dotted line), and 20 °C, solid black line.

Table S1: Length- Mass regressions used for conversion from standard length (SL, in mm) to wet mass (WM, in g). Lower and upper 95% confidence intervals are also given for each coefficient. Regression: WM = *a* SL^b

Species/Genera Name	*a*	*Lower*	*Upper*	*b*	Lower	Upper	R^2
Electrona carlsbergi	2.09 x10^{-05}	9.51 x10^{-06}	4.59 x10^{-05}	2.90	2.72	3.08	0.7214
Electrona antarctica	3.72 x10^{-06}	3.22 x10^{-06}	4.30X10^{-06}	3.27	3.24	3.31	0.9599
Gymnoscopelus fraseri	3.53 x10^{-06}	1.31 x10^{-06}	9.51 x10^{-06}	3.24	3.00	3.47	0.8811
Gymnoscopelus nicholsi	2.87 x10^{-06}	2.02 x10^{-06}	4.08 x10^{-06}	3.25	3.18	3.33	0.9936
Gymnoscopelus braueri	4.58 x10^{-06}	3.60 x10^{-06}	5.82 x10^{-06}	3.11	3.06	3.17	0.9326
Krefftichthys anderssoni	9.05 x10^{-06}	7.49 x10^{-06}	1.09 x10^{-05}	3.02	2.97	3.07	0.9599
Nannobranchium achirus	8.14 x10^{-06}	5.17x 10^{-07}	1.28 x10^{-02}	2.49	1.45	3.54	0.4259
Protomyctophum tenisoni	1.39 x10^{-05}	9.74x 10^{-06}	1.97 x10^{-05}	2.94	2.84	3.03	0.9589
Protomyctophum bolini	1.98 x10^{-05}	1.34 x10^{-05}	2.92 x10^{-05}	2.88	2.77	2.98	0.8926
Protomyctophum choriodon	1.27 x10^{-05}	3.24 x10^{-06}	4.94 x10^{-05}	2.98	2.66	3.30	0.8779
Gymnoscopelus opisthopterus	1.20 x10^{-06}	3.36 x10^{-07}	4.25 x10^{-06}	3.43	3.16	3.71	0.9874
Electrona	3.26 x10^{-06}	2.84 x10^{-06}	3.74 x10^{-06}	3.31	3.28	3.34	0.9563
Gymnoscopelus	4.49 x10^{-06}	3.61 x10^{-06}	5.59 x10^{-06}	3.12	3.07	3.17	0.9351
Protomyctophum	1.24 x10^{-05}	9.89 x10^{-06}	1.55 x10^{-05}	2.99	2.93	3.05	0.9453