

## Contribution to the Themed Section: ‘Mesopelagic resources—potential and risk’ Original Article

# Quantifying carbon fluxes from primary production to mesopelagic fish using a simple food web model

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An ecosystem-based flow analysis model was used to study carbon transfer from primary production (PP) to mesopelagic fish via three groups of copepods: detritivores that access sinking particles, vertical migrators, and species that reside in the surface ocean. The model was parameterized for 40°S to 40°N in the world ocean such that results can be compared with recent estimates of mesopelagic fish biomass in this latitudinal range, based on field studies using acoustic technologies, of ~13 Gt (wet weight). Mesopelagic fish production was predicted to be 0.32% of PP which, assuming fish longevity of 1.5 years, gives rise to predicted mesopelagic fish biomass of 2.4 Gt. Model ensembles were run to analyse the uncertainty of this estimate, with results showing predicted biomass >10 Gt in only 8% of the simulations. The work emphasizes the importance of migrating animals in transferring carbon from the surface ocean to the mesopelagic zone. It also highlights how little is known about the physiological ecology of mesopelagic fish, trophic pathways within the mesopelagic food web, and how these link to PP in the surface ocean. A deeper understanding of these interacting factors is required before the potential for utilizing mesopelagic fish as a harvestable resource can be robustly assessed.

**Keywords:** copepod, detritus, diel vertical migration, mesopelagic fish, mesopelagic food web

## Introduction

Global demand for food is ever increasing, driven by a rising population that is expected to reach nine billion by the year 2050 (Godfray *et al.*, 2010). Mesopelagic fish (the mesopelagic zone has a depth range of 100–1000 m) have been identified as a potential underexploited resource, providing both fishmeal and nutraceutical products such as omega-3 fatty acid dietary supplements for human consumption and the aquaculture industry (St. John *et al.*, 2016 and references therein). Sustainability is a key requirement for the successful exploitation of mesopelagic resources necessitating, at the very minimum, an accurate estimate of the existing biomass of fish inhabiting the mesopelagic ocean. Early estimates of this biomass, based on micronekton net sampling, were ~1 gigatonne (Gt) wet weight (Gjøsæter and Kawaguchi,

1980). It may be, however, that this estimate is too low because mesopelagic fish can avoid pelagic trawls (Kaartvedt *et al.*, 2012). Acoustic methods have more recently been used to evaluate the biomass of mesopelagic fish, with one recent estimate suggesting that the biomass occurring between 40°S and 40°N in the world ocean is ~11–15 Gt (average 13 Gt) (Irigoin *et al.*, 2014). Acoustic estimates exceed those of trawls (Koslow *et al.*, 1997; Kloser *et al.*, 2009; Davison *et al.*, 2015a) although the associated uncertainties are nevertheless substantial, arising from difficulties with interpreting the resonance of gas-filled swim bladders that are present not only in fish, but also other organisms such as siphonophores (Davison *et al.*, 2015b; Kloser *et al.*, 2016).

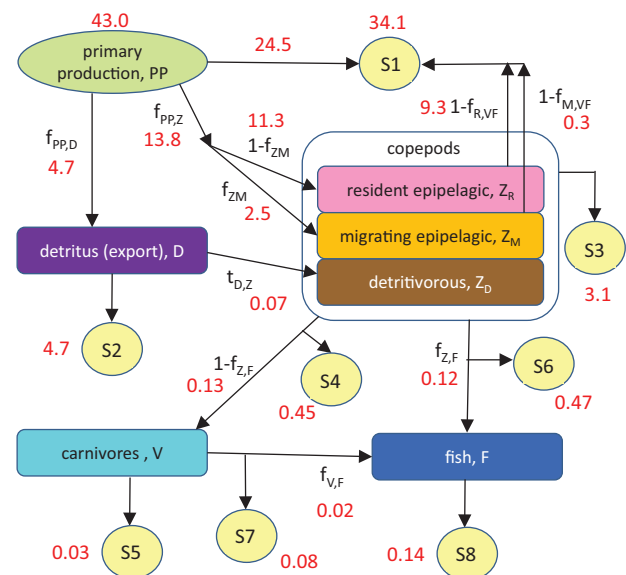
Mesopelagic fish are one of the least well-studied components of marine ecosystems (St. John *et al.*, 2016). The most common

of the mesopelagic fishes are the lanternfish (myctophids), which are ubiquitous throughout the world oceans, with the exception of the Arctic, and which comprise 33 genera and around 245 species (Catul *et al.*, 2011). They feed primarily on planktonic crustaceans such as copepods (Battaglia *et al.*, 2016) and, in turn, provide a source of food for higher trophic levels including squid, mammals and seabirds (Springer *et al.*, 1999; Pereira *et al.*, 2011; Hoving and Robison, 2016). Mesopelagic fish are also an essential prey item for key fishery stocks such as tuna and billfish (Potier *et al.*, 2007; Karakulak *et al.*, 2009). The mesopelagic food web may also play an important role in the sequestration of carbon (C) in the deep ocean and thereby climate regulation (Hudson *et al.*, 2014; Trueman *et al.*, 2014). Many mesopelagic fish undergo diel vertical migration (DVM) to feed in the epipelagic zone (ocean surface to 100 m) at night, descending back to the mesopelagic during the day (Watanabe *et al.*, 1999; Bernal *et al.*, 2015; Klevjer *et al.*, 2016). This migration represents a direct pathway for export of organic C between the surface and deep ocean, along with the production of large fast-sinking faecal material (Davison *et al.*, 2013).

Here, we use an ecosystem-based modelling approach to investigate the trophic pathways that connect primary production (PP) in the surface ocean with C flow through the mesopelagic ecosystem, providing an estimate of the biomass of mesopelagic fish between 40°S and 40°N in the world ocean. The model traces the flows of C from PP through the mesopelagic food web via three groups of copepods: permanent residents of the mesopelagic zone that feed on sinking detritus, vertically migrating organisms, and permanent residents of the epipelagic. Results are discussed in context of the many uncertainties associated with the functioning of the mesopelagic ecosystem, highlighting areas in particular need of future research in order to assess the potential sustainability of mesopelagic fish as a harvestable resource.

## Model description and methods

A flow diagram of the model, illustrating the trophic pathways from PP to mesopelagic fish, is shown in Figure 1 along with a list of variables and parameters in Tables 1 and 2. The model is a flow analysis, assumes steady state and does not calculate stocks, with the exception of mesopelagic fish. It is parameterized to represent a generalized ecosystem between 40°S to 40°N in the world ocean so that results can be directly compared with field-based estimates of mesopelagic fish biomass of ~13 Gt for this latitudinal range (Irigoin *et al.*, 2014). The model tracks the flows of C from PP to mesopelagic fish via copepods and their carnivorous invertebrate predators. Given that the fish undertake DVM, food sources within both the mesopelagic and epipelagic zones are considered. Three types of copepods are distinguished: detritivores,  $Z_D$ , that are permanent residents of the mesopelagic zone and which feed on sinking particles (detritus, D), migratory copepods,  $Z_M$ , which, like the mesopelagic fish, feed in epipelagic waters by night and descend in the water column by day to escape predation (Zaret and Suffern, 1976; Hays, 2003) and permanent residents of the epipelagic,  $Z_R$ , that feed on phytoplankton and the associated microzooplankton assemblage. All three groups are grazed not only by the fish, but also by invertebrate carnivores (V) which represent a wide variety of organisms including amphipods, chaetognaths and jellyfish (Tönnesson and Tiselius, 2005; Daewel *et al.*, 2014). Both copepods and invertebrate carnivores constitute prey for the mesopelagic fish.



**Figure 1.** Flow diagram of the model showing pathways from PP to fish (with  $f_X$  parameters specifying fractional division of fluxes). Sinks for C are: S1 remineralisation of C and loss to higher trophic levels in the epipelagic zone; S2 detritus-associated losses; S3 respiration and egestion by  $Z_M$ ,  $Z_R$ ; S4 respiration and egestion by invertebrate carnivores; S5 non-fish carnivore losses to higher trophic levels; S6 respiration and egestion by fish (zooplankton as food); S7 respiration and egestion by fish (carnivores); S8 fish mortality. Flows (Gt C year<sup>-1</sup>) are shown in red for the steady state solution of the model (see “Results” section).

**Table 1.** Model variables.

Variable	Definition	Unit of measure
$G_{Z(D)}$	Copepod production: detritivores	Gt C year <sup>-1</sup>
$G_{Z(M)}$	Copepod production: vertical migrators	Gt C year <sup>-1</sup>
$G_{Z(R)}$	Copepod production: resident epipelagic	Gt C year <sup>-1</sup>
$R_Z$	Copepod food available to V, F	Gt C year <sup>-1</sup>
$G_V$	Invertebrate carnivore production	Gt C year <sup>-1</sup>
$G_F$	Mesopelagic fish production	Gt C year <sup>-1</sup>
$L_F$	Loss rate of fish	Gt C year <sup>-1</sup>
$B_F$	Mesopelagic fish biomass	Gt wet weight

The starting point of the analysis is PP, which is specified as a fixed rate, PP (Gt C year<sup>-1</sup>). Satellite-based estimates of PP between 40°S and 40°N were extracted from original published fields for a range of algorithms, giving 46.3 (Behrenfeld and Falkowski, 1997), 63.3 (Carr, 2002), 47.9 (Marra *et al.*, 2003), and 43.0 Gt C year<sup>-1</sup> (Westberry *et al.*, 2008). We use the last of these, which is based on the most sophisticated and up-to-date methodology, giving PP = 43 Gt C year<sup>-1</sup>. A fraction of PP,  $f_{PP,D}$ , is exported from the surface ocean to the mesopelagic as detritus, providing a food supply for detritivorous zooplankton. Empirical estimates of export ratio (e-ratio = export/PP =  $f_{PP,D}$ ) averaged between 40°S and 40°N, again extracted from the original data for different algorithms, are variable: 0.091 (Dunne *et al.*, 2005), 0.033 (Henson *et al.*, 2011), and 0.099 (Siegel *et al.*, 2014). Estimates from global biogeochemical models include 0.128 (Moore *et al.*, 2004), 0.198–0.199 (Collins *et al.*, 2011), 0.067–0.077 (Dunne *et al.*, 2012, 2013), and 0.145–0.179 (Séférian *et al.*, 2013).

**Table 2.** Model parameters (Group 1: relatively certain; Group 2: relatively uncertain).

Parameter	Definition	Default value (range)	Unit of measure
Group 1 (varied $\pm 50\%$ in the ensemble uncertainty analysis)			
PP	PP	43 (43–63)	Gt C year <sup>-1</sup>
$f_{PP,D}$	Frac. PP exported as detritus	0.11 (0.033–0.199)	Dimensionless
$f_{PP,Z}$	Frac. PP to copepods	0.32 (0.25–0.47)	Dimensionless
$f_{ZM}$	Frac. $f_{PP,Z}$ due to migrators	0.18 (0.12–0.22)	Dimensionless
$K_Z$	GGE: copepods	0.26 (0.13–0.32)	Dimensionless
$K_V$	GGE: carnivores	0.22 (0.10–0.51)	Dimensionless
$K_F$	GGE: fish	0.2 (0.18–0.21)	Dimensionless
Group 2 (varied $\pm 75\%$ in the ensemble uncertainty analysis)			
$t_{D,Z}$	Transfer eff.: detritus to copepods	0.0145	Dimensionless
$f_{M,VF}$	Frac. migrating copepods to V, F	0.88	Dimensionless
$f_{R,VF}$	Frac. resident copepods to V, F	0.18	Dimensionless
$f_{Z,F}$	Frac. copepods grazed by fish	0.5	Dimensionless
$f_{V,F}$	Frac. carnivores grazed by fish	0.8	Dimensionless
$m_F$	Mesopelagic fish mortality	0.67	Year <sup>-1</sup>

Ranges of Group 1 parameters, as described in the text, are listed in brackets. No ranges are given for Group 2 parameters because these are highly uncertain (see text).

Parameter  $f_{PP,D}$  was estimated as an average of these values, giving 0.11.

Sinking detritus is acted upon by bacteria and zooplankton in the mesopelagic zone, diminishing the flux with depth and remineralising nutrients and C to their inorganic forms (Steinberg *et al.*, 2008; Giering *et al.*, 2014). It may be that the primary source of nutrition for detritivorous zooplankton is not the non-living detrital matrix, which is refractory in nature but, rather, microbes that colonize the detritus and which are rich in nutrients such as essential fatty acids (Lampitt *et al.*, 1990; Mayor *et al.*, 2014; Anderson *et al.*, 2017). It is therefore difficult to specify a growth efficiency for zooplankton grazing on detritus because of the separate contributions of microbial and refractory substrates and the associated differential ingestion and utilization thereof. Instead, we apply a simple trophic transfer efficiency,  $t_{D,Z}$ , which represents the aggregate outcome of detritus utilization, quantifying the fraction of exported detritus, including associated microbes, that is assimilated into the biomass of mesopelagic zooplankton. Copepod growth accruing from the detrital pathway,  $G_{Z(D)}$  is then:

$$G_{Z(D)} = t_{D,Z} f_{PP,D} PP. \quad (1)$$

The nutrition of detritivorous zooplankton in the mesopelagic zone was investigated by Anderson *et al.* (2017) using a stoichiometric model that has C and an essential fatty acid as currencies, and which includes the separate roles of detritus-attached microbes and the raw detrital substrate. Results indicated that feeding on microbes is likely a favourable strategy, despite low microbial biomass. Transfer of C to zooplankton was remarkably low because of trophic losses within the microbial food web prior to ingestion, with a typical value of 1.45%, i.e.  $t_{D,Z} = 0.0145$ . This value is much lower than growth efficiencies for zooplankton grazing detritus as applied in previous mesopelagic ecosystem models, e.g. 0.23 (Anderson and Tang, 2010; Giering *et al.*, 2014). We therefore investigate the sensitivity of model-predicted mesopelagic fish biomass to parameter  $t_{D,Z}$ .

Mesopelagic fish feed on herbivorous, omnivorous and carnivorous copepods, both residents of the epipelagic and those undergoing DVM. The starting point of quantifying these pathways is

to calculate the fraction of PP that is consumed by copepods, parameter  $f_{PP,Z}$ . It has been estimated that mesozooplankton directly consume 10–15% of PP (Behrenfeld and Falkowski, 1997; Calbet, 2001), giving a mid-range value of 12%. However, this excludes indirect routes, notably via microzooplankton. Steinberg and Landry (2017) constructed a C budget of the global ocean ecosystem and estimated that 66% of PP is consumed by microzooplankton, with a further 10% of PP accounting for consumption of bacterial secondary production, giving a total intake by microzooplankton of 76% of PP. If the gross growth efficiency (GGE) for microzooplankton is 0.3 (Straile, 1997), and mesozooplankton grazing is the primary loss term for microzooplankton, the fraction of PP reaching mesozooplankton via these routes is  $0.76 \times 0.3 = 0.23$ . When added to direct consumption of 0.12, this results in mesozooplankton consumption of 35% of PP. Copepod grazing can also be estimated from the predictions of global biogeochemical models, most of which today distinguish between micro- and mesozooplankton. Mesozooplankton grazing of between 19 and 11.2 Gt C year<sup>-1</sup> was predicted using different versions of the PISCES model by Buitenhuis *et al.* (2006) and Aumont *et al.* (2015), respectively, which convert to fractions of PP of 0.27 and 0.25 (based on PP of 69.7 vs. 44.3 Gt C year<sup>-1</sup> for the two models). A similar value can be calculated from the results of the COBAL model as published in Stock *et al.* (2014), with mesoplankton grazing and PP of 13.4 and 51.9 Gt C year<sup>-1</sup>, respectively, giving grazing/PP = 0.26. On the other hand, a considerably higher ratio, 0.47, is generated by the MEDUSA model (Yool *et al.*, 2013), caused by a relatively high grazing on non-diatoms. We use a mean of the estimates described earlier, giving  $f_{PP,Z} = 0.32$ .

The efficiency with which copepod consumption of PP,  $f_{PP,Z}$ , is transferred to the mesopelagic ecosystem depends on whether the copepods undergo DVM or not. Migrating copepods are tightly coupled to, and indeed part of, the mesopelagic ecosystem given that many of the invertebrate carnivores and mesopelagic fish themselves undergo DVM. On the other hand, non-migrating copepods may contribute relatively little to the mesopelagic ecosystem if they are largely consumed by epipelagic resident predators. The migrating fraction of total mesozooplankton biomass is commonly estimated as the difference between day



and night measurements in surface waters. Variability is inevitably seen between locations and seasons, including estimates of 0.14–0.68, mean 0.37 (equatorial Pacific: Zhang and Dam, 1997), 0.41 (Sargasso Sea: Madin et al., 2001), 0.35–0.53, mean 0.41 (subtropical Pacific: Al-Mutairi and Landry, 2001), 0.29 and 0.44 for copepods (subtropical and subarctic Pacific respectively: Steinberg et al., 2008), and 0.06–0.40 (Mediterranean: Isla et al., 2015). Averaging all these results yields a migrating fraction of 0.37. Parameter  $f_{ZM}$  in the model is the fraction of total copepod grazing in the epipelagic zone that is attributable to migrating animals. This depends not only on migrator biomass, but also on the duration of feeding in surface waters. The simplest assumption is that migrators spend, on average, 50% of the day (the night hours) feeding in surface waters and so their relative contribution to grazing PP, per unit biomass, is half compared with non-migrating animals. Thus,  $f_{ZM} = 0.37 \times 0.5 = 0.18$ .

The growth of migrating and resident epipelagic copepods,  $G_{Z(M)}$  and  $G_{Z(R)}$ , are now:

$$G_{Z(M)} = f_{PP,Z} f_{ZM} K_Z PP, \quad (2)$$

$$G_{Z(R)} = f_{PP,Z} (1 - f_{ZM}) K_Z PP, \quad (3)$$

where  $K_Z$  is copepod GGE. We use  $K_Z = 0.26$  (a typical range is 0.13–0.32; Straile, 1997).

Copepods, both migrating and resident in the epipelagic zone, provide food not only for migrating fish and carnivorous invertebrates, but also for higher trophic levels that reside in near-surface waters (Springer et al., 2007; Bachiller et al., 2016). For the purpose of calculating carbon transfer from copepods to higher trophic levels, we assume that the biomass of migrating predators as a fraction of total predators (migrators and epipelagic residents) is 0.37 (no estimates exist), i.e. equal to the corresponding fraction for copepods, and that migrating predators spend an average of 50% of their time in surface waters. The fractional loss of epipelagic resident (non-migratory) copepods that is due to grazing by migrating predators (fish and invertebrates), parameter  $f_{R,VF}$ , is then equivalent to  $f_{ZM}$ , i.e.  $f_{R,VF} = 0.18$ . In contrast, the fractional loss of migrating copepods to migrating predators, parameter  $f_{M,VF}$ , should be high given the synchrony in behaviour of the two communities. Moreover, if epipelagic resident predators rely on visual cues for feeding then, at least in theory, their grazing on migrating copepods should be zero if the copepods avoid surface waters during daylight hours by DVM. Migrating copepod species do, however, contribute to the diets of epipelagic fish (Beaugrand et al., 2003; Garrido et al., 2015; Bachiller et al., 2016). These fish have evolved complex adaptations to detect prey in dimly lit waters, notably large upward-facing eyes (Gagnon et al., 2013). Feeding may follow a bimodal cycle whereby zooplankton are most effectively captured at dawn and dusk as they migrate to and from surface waters (Allison et al., 1996; Cardinale et al., 2003). As a first approximation, we assume that epipelagic predators access migrating copepods as food for 1 h at either end of the day (dawn and dusk), whereas migrating predators have continuous access. Taking into consideration the relative biomass of the two predator communities (0.37 and 0.63 for migrators and epipelagic residents, respectively), the relative grazing by migrating and epipelagic resident predators on migrating copepods are 0.37 and 0.052 ( $=0.63 \times 2/24$ ), giving

$f_{M,VF}$  (the grazing by migrating predators on migrating copepods) as  $0.37/(0.37 + 0.052) = 0.88$ .

The total amount of copepod food available to migrating fish and carnivorous invertebrates,  $R_Z$ , is now:

$$R_Z = G_{Z(D)} + f_{M,VF} G_{Z(M)} + f_{R,VF} G_{Z(R)}. \quad (4)$$

There are no data and so we tentatively assume that the fraction of  $R_Z$  that is consumed by mesopelagic fish, parameter  $f_{Z,F}$ , is 0.5, with the remainder,  $1 - f_{Z,F}$ , consumed by invertebrate carnivores whose growth,  $G_V$ , is:

$$G_V = (1 - f_{Z,F}) K_V R_Z, \quad (5)$$

where  $K_V$  is invertebrate carnivore GGE. A number of values of GGE for amphipods and decapods have been published: 0.15–0.18 (Dagg, 1976), 0.16 (Ikeda, 1991) and 0.20–0.51 (Yamada and Ikeda, 2006). Values for gelatinous organisms also show considerable variation, from values around 0.1 (Larson, 1987; Möller and Riisgård, 2007; Möller et al., 2010) to over 0.3 (Reeve et al., 1989; Costello, 1991). We use an average of the above values,  $K_V = 0.22$ . The fraction of invertebrate carnivore losses to mesopelagic fish was assumed to be high,  $f_{V,F} = 0.8$ ; we will show that the model is not sensitive to this parameter. The production of mesopelagic fish,  $G_F$ , can now be calculated as the sum of terms representing ingestion of copepods and invertebrate carnivores:

$$G_F = K_F (f_{Z,F} R_Z + f_{V,F} G_V), \quad (6)$$

where  $K_F$  is fish GGE. Ikeda (1996) investigated the metabolism and energy budget of the mesopelagic fish *Maurollicus muelleri* and estimated a GGE of 0.18. Transfer efficiency for secondary to tertiary consumers in the pelagic ecosystem of the Oyashio Region was subsequently estimated by Ikeda et al. (2008) to be 0.21. We use  $K_F = 0.20$ .

By assuming that the system is in steady state, the biomass (wet weight) of mesopelagic fish,  $B_F$ , can be estimated by dividing production by the fish mortality rate,  $m_F$ :

$$B_F = G_F \sigma / m_F, \quad (7)$$

where the conversion coefficient,  $\sigma$ , is 11.9 g wet weight per g C dry weight based on conversions of 0.20 for dry: wet weight and 0.42 for C as fraction dry weight (Ikeda et al., 2011). The longevity of mesopelagic fish is typically recorded as being between 1 and 2 years (Bystydzińska et al., 2010; Linkowski et al., 1993; Takagi et al., 2006; Hosseini-Shekarabi et al., 2015), although sometimes up to 3 or 4 years at high latitudes (Halliday, 1970; Gjøsæter, 1973; Greely et al., 1999; Saunders et al., 2015). We use a fish mortality rate of  $m_F = 1/1.5 = 0.67 \text{ year}^{-1}$ , but will examine the sensitivity of  $B_F$  to this parameter.

The model was first investigated with default parameter settings (Table 2). The uncertainty of the predicted biomass of mesopelagic fish associated with model parameters was then assessed in two ways. First, a standard sensitivity analysis was carried out in which individual parameters were varied, in turn,  $\pm 50\%$ . Second, an ensemble analysis was undertaken in which model solutions were generated throughout the entire 13D parameter space, randomly assigning values for each parameter within specified ranges. For this purpose, model parameters were divided into two groups (Table 2) based on our experiences parameterising

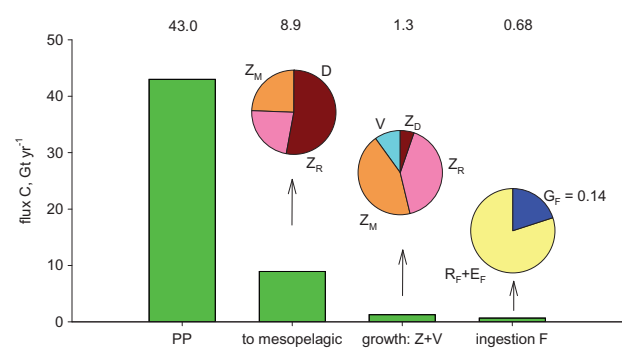
the model: Group 1 (relatively certain) could be constrained with some confidence from the literature, whereas Group 2 (relatively uncertain) are poorly known and weakly constrained. In effect, this is a process of expert elicitation that is often used in constructing Bayesian frameworks (Choy *et al.*, 2009; Krueger *et al.*, 2012). Group 1 parameters are: PP, the fractions of PP to detritus and copepods ( $f_{PP,D}$  and  $f_{PP,Z}$ ), the fraction of  $f_{PP,Z}$  attributable to migrators ( $f_{ZM}$ ) and the growth efficiencies for copepods, invertebrate carnivores and mesopelagic fish ( $K_Z$ ,  $K_V$ , and  $K_F$ ). Group 2 parameters are:  $t_{D,Z}$  (transfer efficiency of detritus utilization by copepods), trophic pathway partitioning parameters  $f_{M,VF}$  (migrating copepods to mesopelagic V, F),  $f_{R,VF}$  (epipelagic resident copepods to mesopelagic V, F),  $f_{Z,F}$  (copepod fraction to mesopelagic fish),  $f_{V,F}$  (invertebrate carnivore fraction to mesopelagic fish) and, finally,  $m_F$  (the mortality rate of mesopelagic fish). Group 1 parameters were varied  $\pm 50\%$  in the ensemble uncertainty analysis, while Group 2 parameters were varied  $\pm 75\%$ . These are wide limits and, if anything, should overestimate the total uncertainty associated with predicting  $B_F$ . The chosen percentages are subjective but, nevertheless, we believe generally representative based on our experience of parameterising the model from the literature.

The model is set up in a Microsoft Excel spreadsheet, which is available on request from the first author.

## Results

The model was first run with default parameters (Table 2), including input PP of 43 Gt C year<sup>-1</sup>. Predicted C fluxes from PP to fish are shown in Figure 2 (see also the steady state solution of the model as shown in Figure 1). The majority of PP is remineralized or lost to epipelagic predators, with only 21% (8.9/43) predicted to supply the mesopelagic ecosystem via sinking detritus (11%; parameter  $f_{PP,D}$ ), vertically migrating copepods (5.1%; the product  $f_{PP,Z} f_{ZM} f_{M,VF}$ ) and resident epipelagic copepods (4.7%;  $f_{PP,Z}(1-f_{ZM})f_{R,VF}$ ). The total production of the prey of mesopelagic fish, i.e. copepods and invertebrate carnivores, is 1.3 Gt C year<sup>-1</sup>, most of which is due to migrant and resident epipelagic copepods that have direct access to PP. The predicted contribution via detritivorous copepods is small ( $G_{Z(D)} = 0.07$  Gt C year<sup>-1</sup>) because of the low trophic transfer efficiency ( $t_{D,Z} = 0.0145$ ) associated with using refractory detritus as a source of food. Likewise, the predicted contribution of invertebrate carnivores to mesopelagic fish diet is low ( $G_V = 0.13$  Gt C year<sup>-1</sup>) because these animals are one trophic level above the copepods. The mesopelagic fish consume 0.68 Gt C year<sup>-1</sup> of the 1.3 Gt C year<sup>-1</sup> available to them (the remainder goes to other predators), equivalent to 1.6% of PP. With a growth efficiency,  $K_F$ , of 0.2, the predicted production of mesopelagic fish is 0.14 Gt C year<sup>-1</sup>, i.e. 0.32% of PP. Mesopelagic fish biomass can now be estimated as the quotient production/mortality ( $G_F/m_F$ ; Equation 7). Using  $m_F = 0.67$  year<sup>-1</sup> (Table 2), which equates to a fish longevity of 1.5 years, predicted mesopelagic fish biomass is 2.4 Gt C wet weight (11.9 g wet weight per g C dry weight).

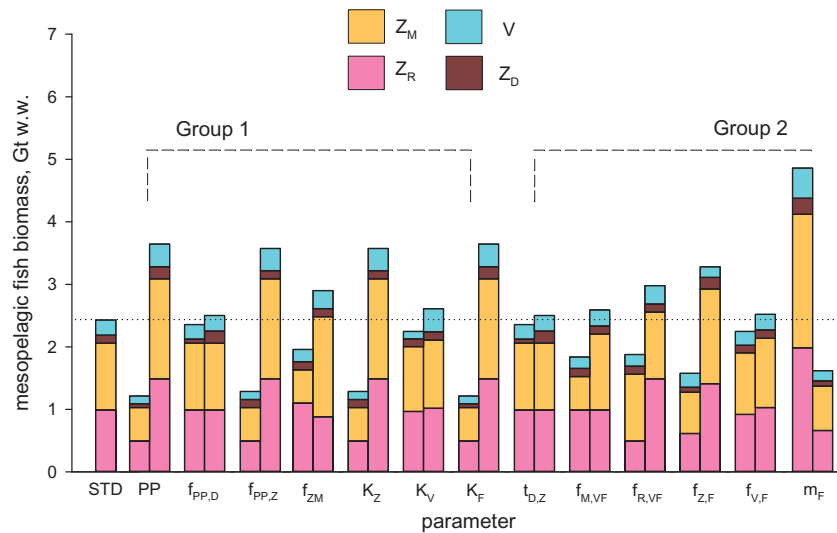
Parameter sensitivity analysis was carried out using predicted mesopelagic fish biomass,  $B_F$ , as the focus because fish represent the apex of the model ecosystem. Each parameter was varied, in turn,  $\pm 50\%$  (Figure 3). Predicted  $B_F$  shows relatively high sensitivity to several Group 1 (relatively certain) parameters: PP,  $f_{PP,Z}$ ,  $K_Z$ , and  $K_F$ . Model sensitivity to these parameters is unsurprising given that PP provides the source of C entering the system,  $f_{PP,Z}$  specifies the fraction of PP utilized by copepods, (the main vector



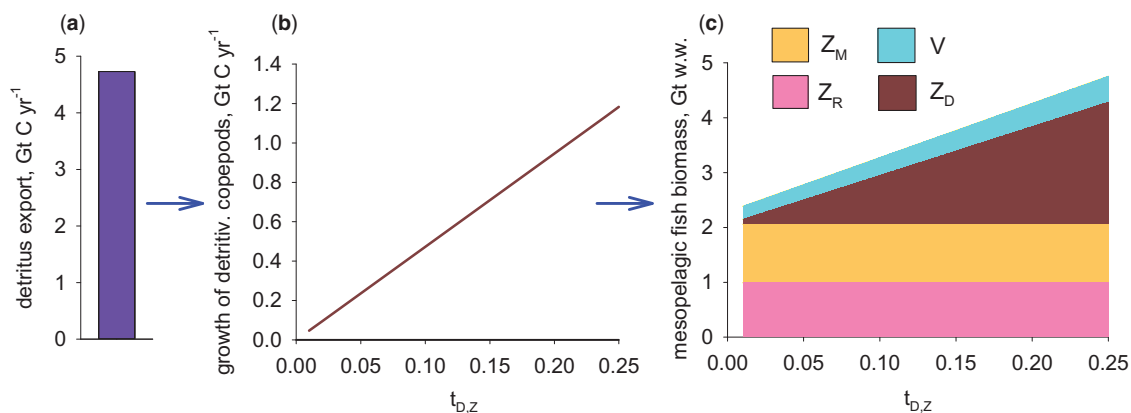
**Figure 2.** Predicted fluxes of carbon from PP to fish. Columns are (left to right): (1) PP; (2) C supply to the mesopelagic ecosystem; pie chart shows relative contributions via detritus, D, migrating and epipelagic resident copepods (those animals that act as food for mesopelagic invertebrate carnivores and fish),  $Z_M$  and  $Z_R$  respectively; (3) mesopelagic fish food sources (growth of); pie chart shows allocation between copepods,  $Z_D$  (detritivorous copepods),  $Z_M$ ,  $Z_R$  and invertebrate carnivores, V; (4) C flux to fish; pie chart shows growth,  $G_F$ , vs. respiration plus egestion,  $R_F + E_F$ . Figures at top are numerical values for the heights of the bars.

of transfer between the epipelagic and mesopelagic ecosystems) and  $K_Z$  and  $K_F$  are the growth efficiencies of copepods and mesopelagic fish, respectively. Regarding Group 2 parameters (relatively uncertain), predicted  $B_F$  shows moderate sensitivity to parameters  $f_{M,VF}$  and  $f_{R,VF}$ , which specify the fractions of migrating and epipelagic resident copepods grazed by migrating predators, i.e. invertebrate carnivores and mesopelagic fish (with the remainder providing food for epipelagic resident predators). Sensitivity is also seen for parameter  $f_{Z,F}$ , which quantifies the fraction of that grazing utilized by mesopelagic fish (rather than invertebrate carnivores), but not  $f_{V,F}$  because, as noted earlier, invertebrate carnivores are only a minor food source for the fish. A notable result is that the sensitivity analysis indicates low sensitivity for parameter  $f_{PP,D}$ , the fraction of PP exported as detritus, because the detrital substrate is utilized for growth by detritivorous copepods with low efficiency (0.0145; parameter  $t_{D,Z}$ ). These zooplankton therefore contribute only a small fraction of mesopelagic fish diet. Finally, predicted  $B_F$  is unsurprisingly sensitive to fish mortality rate,  $m_F$ . For example, halving  $m_F$  to 0.335 per year, which is equivalent to increasing fish longevity from 1.5 to 3 years, leads to predicted mesopelagic fish biomass increasing from 2.4 to 4.9 Gt.

Uncertainty associated with parameter values depends not only on sensitivity, as described above, but also on the intrinsic difficulty in assigning parameter values from the literature, as per the division of parameters into Groups 1 and 2. Of particular note in this regard is parameter  $t_{D,Z}$ , the trophic transfer efficiency for copepods utilizing detritus as a food source. Our default value of 0.0145 is based on the recent modelling study of Anderson *et al.* (2017), whereas previous studies (Anderson and Tang, 2010; Giering *et al.*, 2014) have used a transfer efficiency of 0.23, i.e. more than an 15-fold higher. If this value is used here for parameter  $t_{D,Z}$ , exported detritus is then predicted to become a significant source of C fuelling the mesopelagic ecosystem: the growth of detritivorous zooplankton increases from 0.07 to 1.1 Gt C year<sup>-1</sup>, the contribution of these zooplankton to the diet of mesopelagic fish increases from 5 to 42% and predicted mesopelagic fish biomass increases from 2.4 to 4.6 Gt (Figure 4).



**Figure 3.** Sensitivity of predicted mesopelagic fish biomass (Gt wet weight) to model parameter values  $\pm 50\%$  (with maximum bound of 1.0 for parameters  $f_{M,VF}$  and  $f_{V,F}$ ). Parameters are divided between Group 1 (relatively certain) and Group 2 (relatively uncertain). STD is standard run (parameters as in Table 2). Colours show relative contributions of copepods ( $Z_M$ , migrating copepods;  $Z_R$ , copepods that reside in the epipelagic;  $Z_D$ , detritivorous copepods) and carnivorous invertebrates (V) to fish diet.

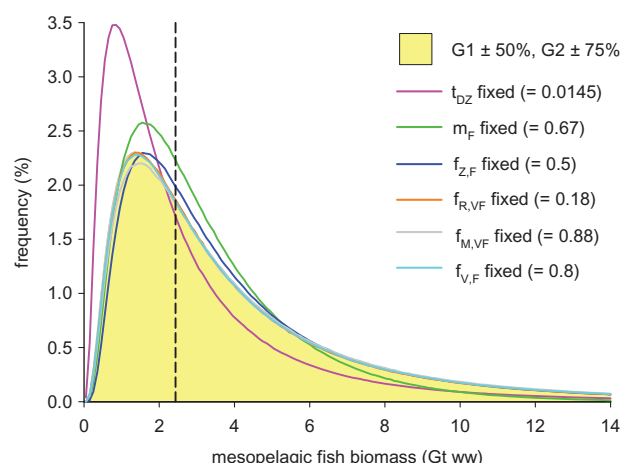


**Figure 4.** Model sensitivity to transfer efficiency for copepods utilizing detritus (parameter  $t_{D,Z}$ ): (a) detritus export,  $\text{Gt C yr}^{-1}$ ; (b) growth of detritivorous copepods; (c) mesopelagic fish biomass showing contributions of different food sources:  $Z_R$ ,  $Z_M$ ,  $Z_D$ , and V to production (colours as in Figure 3).

The overall uncertainty in predicted mesopelagic fish biomass due to model parameterization depends on the combined uncertainties associated with the parameters in total. We therefore undertook ensemble analyses of the model, with each ensemble consisting of  $10^7$  runs. Parameter values for each run were randomly generated within specified ranges. In the case of Group 1 (relatively certain) parameters, this was  $\pm 50\%$ , and for Group 2 parameters (relatively uncertain) it was  $\pm 75\%$ . Parameter  $t_{D,Z}$  was treated differently based on the analysis shown in Figure 4. When varying Group 2 parameters  $\pm 75\%$ ,  $t_{D,Z}$  was varied between its standard value, 0.0145, and 0.23. Varying parameters  $f_{M,VF}$  and  $f_{V,F}$   $\pm 75\%$  leads to values  $>1$ , which are not permissible; in this event, parameter values were reset equal to 1. Predictions for mesopelagic fish biomass were allocated within 0.1 Gt bins, which were then plotted as a frequency distribution. Results (Figure 5) exhibit strong positive skew, showing that it is possible to predict  $B_F$  significantly higher than our standard value of 2.4 Gt (default parameter settings: Table 2). Nevertheless, only

27% of predictions exceed 5 Gt biomass, and only 8% exceed 10 Gt. The predicted frequency distribution widens if both Groups 1 and 2 parameters are varied within ranges  $\pm 75\%$  (Figure 5), although even here only 26 and 10% of the distribution exceeds 5 and 10 Gt, respectively. Note that the mode of the frequency distribution shifts to the left because the relative contribution of parameter  $t_{D,Z}$  to overall uncertainty is diminished (this parameter is only increased, rather than varied  $\pm$ ); the mode of a frequency distribution where numbers are multiplied together (as is the case for model parameters) is generally less than the mean. If, on the other hand, all parameters are varied  $\pm 50\%$  (with the range for parameter  $t_{D,Z}$  scaled in proportion), the frequency distribution narrows somewhat, with 23 and 2% of predictions for  $B_F$  exceeding 5 and 10 Gt, respectively.

Finally, the relative contributions of the least well constrained parameters (those of Group 2) to overall uncertainty in predicted mesopelagic fish biomass was investigated in greater detail. Returning to the baseline analysis in which parameters in Groups



**Figure 6.** Effect of fixing Group 2 (relatively uncertain) parameters, in turn, to their standard values (Table 2) on the ensemble predictions. Yellow-shaded area is the frequency distribution with all parameters included (as in Figure 5). Frequency distributions with parameters excluded are:  $t_{D,Z}$  (pink line),  $m_F$  (green),  $f_{Z,F}$  (blue),  $f_{R,VF}$  (orange),  $f_{M,VF}$  (grey), and  $f_{V,F}$  (cyan).

commercial fish species such as herring, plaice and sole, which are often between 0.05 and 0.1% of PP (Nielsen and Richardson, 1996; Sommer *et al.*, 2002; Chassot *et al.*, 2007, 2010). Pauly and Christensen (1995) estimated global fish catch to be 0.21% of PP, although this estimate showed wide variation when separated into different ecosystem types with values, for example, of 0.01 and 2.3% for open ocean and upwelling ecosystems, respectively. Large variations in fish catch as a percentage of PP are to be expected between ecosystems because different food webs have different size structures and numbers of trophic levels (Ryther, 1969; Pauly and Christensen, 1995; Jennings and Collingridge, 2015; Stock *et al.*, 2017). Furthermore, fish catch need not necessarily be a good indicator of population biomass because of discards, the efficiency of nets, selective catch of different species, etc. Even if the production of mesopelagic fish is only 0.32% of PP, this may provide potential as a harvestable resource. Quantifying mesopelagic fish biomass is also a useful indicator, especially as the model estimate can be compared with those from field studies. Additional factors that need to be taken into consideration when considering harvestable potential include a knowledge of controlling mechanisms, a holistic understanding of the community, and ecological concerns associated with harvesting a significant, but poorly understood, component of marine food webs (St. John *et al.*, 2016).

The modelling work presented herein emphasizes the importance of migrating animals in the transfer of C from the surface ocean to the mesopelagic zone. It also highlights major gaps in our knowledge of the ecology and trophodynamics of mesopelagic ecosystems and their associated links to PP, gaps that are not easy to fill because food web interactions in the mesopelagic zone are difficult to measure (Robinson *et al.*, 2010). The knowledge gaps may be divided into four areas: (i) trophic linkages between copepods and both migrating and non-migrating (epipelagic resident) predators, (ii) mesopelagic fish diet, (iii) mesopelagic fish growth efficiency and mortality (longevity), and (iv) the efficiency of detritus utilization as a food source by mesopelagic zooplankton. These are now discussed in turn:

Despite the relatively short food chain, model results indicated that just 1.6% of PP ends up being ingested by mesopelagic fish and, combined with a gross growth efficiency of 0.2, 0.32% of PP accrues as mesopelagic fish production. In fact, this percentage is relatively high compared with estimates of fish catches of



(i) The relative extent to which migrating copepods are consumed by migrating predators vs. epipelagic predators depends on the relative abundances of the two predator groups and the amount of time that predators and prey are co-located. The predator groups represent a diverse array of organisms, including fish and invertebrate carnivores, and so specifying their relative abundances is difficult. For simplicity, we assumed that the ratio of migrating to non-migrating predators is the same as for copepods, which could be estimated from data. Most of the mesopelagic fauna undergo diel migration (Angel and Pugh, 2000; Siegelman-Charbit and Planque, 2016), including the fish and invertebrate carnivores (Clarke, 1980; Catul *et al.*, 2011; Bernal *et al.*, 2015). We therefore assumed that these migrating predators have continuous access to migrating copepod prey, the two communities operating in concert. Quantifying the extent to which migrating copepods are grazed by the epipelagic resident predator community is, however, considerably more problematic. Grazing would be zero if DVM was a perfect predator avoidance strategy, but it is not. Migrating copepods are known to contribute significantly to the diets of epipelagic fish (Beaugrand *et al.*, 2003; Garrido *et al.*, 2015; Bachiller *et al.*, 2016). Feeding may occur primarily during the hours of dawn and dusk as the migrators travel to and from surface waters (Allison *et al.*, 1996; Cardinale *et al.*, 2003). We made the simplifying assumption in the model that epipelagic predators gain access to the migrating copepods for an average of 1 h at either end of each day. One interesting complication, for example, is that moonlight may expose migrating organisms to predation. Indeed, it appears that they may counter this threat by avoiding surface waters at night during full moon (Last *et al.*, 2016).

(ii) Having determined the extent to which copepods are grazed by the migrating predator community as a whole, there is still the difficulty of specifying the fraction that is exploited by the mesopelagic fish (vs. the invertebrate carnivores). We made the simple assumption that mesopelagic fish are responsible for 50% of copepod losses (parameter  $f_{Z,F}$ ), along with 80% of invertebrate carnivore losses (parameter  $f_{V,F}$ ), highlighting the difficulty in deriving quantitative estimates of trophic pathway parameters. Based on this assumption, our results indicated that copepods account for 85% of the mesopelagic fish diet. The predicted relative contributions were 5% from mesopelagic detritivorous copepods, 41% from migrating copepods and 39% from epipelagic resident copepods. It is well known that mesopelagic fish, including myctophids, feed on crustaceans (Clarke, 1980; Van Noord *et al.*, 2016), often with a predominance of copepods (Kawaguchi and Mauchline, 1982; Pepin, 2013; Bernal *et al.*, 2015; Saunders *et al.*, 2015). Other prey items include gelatinous zooplankton (Bystydzińska *et al.*, 2010; Hudson *et al.*, 2014). Estimates of myctophid fish trophic position derived from stable isotope analysis of nitrogen ( $\delta^{15}\text{N}$ ) in bulk tissues (Cherel *et al.*, 2010) and individual amino acids (Choy *et al.*, 2015; Hetherington *et al.*, 2017) vary from 3.3 to 4.2, indicating that these fish are secondary and tertiary consumers. Model results were thus generally consistent with this trophic positioning.

(iii) Model predictions for the biomass of mesopelagic fish are directly influenced by fish growth efficiency and mortality rate ( $K_F$  and  $m_F$ , respectively) and so it is unsurprising that results are sensitive to these parameters. We used a fish GGE of 0.20 (Ikeda, 1996; Ikeda *et al.*, 2008). Similar values of growth efficiency have been recorded in commercial fish species such as cod, haddock and herring (Peck *et al.*, 2003, 2015; Bernreuther *et al.*, 2013),

although higher values nearer 0.3 are also seen (e.g., Björnsson and Tryggvadóttir, 1996; Sogard and Olla, 2001; Bernreuther *et al.*, 2013). Predicted mesopelagic fish biomass is particularly sensitive to the parameterization of fish longevity. We used a default mortality of  $0.67\text{ year}^{-1}$  which is equivalent to life span of 1.5 years (Bystydzińska *et al.*, 2010; Lingkowski *et al.*, 1993; Tagaki *et al.*, 2006; Hosseini-Shekarabi *et al.*, 2015). If longevity is increased to 3 years (Halliday, 1970; Gjøsæter, 1973; Greely *et al.*, 1999; Saunders *et al.*, 2015), predicted fish biomass doubles from 2.4 to 4.9 Gt. Note that uncertainty in mortality rate does not influence predicted mesopelagic fish production.

(iv) A perhaps surprising outcome of our analysis is that detritivorous zooplankton are predicted to contribute only 5% to the diet of mesopelagic fish. This occurred because of the low trophic transfer efficiency for copepods grazing on detritus, 1.45% (parameter  $t_{D,Z} = 0.0145$ ). Detritus is made up of refractory compounds that are depleted in micronutrients including amino acids and fatty acids (Mann, 1988; Cowie and Hedges, 1996; Mayor *et al.*, 2011). It is however colonized by micro-organisms that provide substrates that are readily absorbed and which are rich in these micronutrients (Phillips, 1984). A favourable strategy for detritivorous copepods may therefore be to selectively utilize these micro-organisms as a source of nutrition (Mayor *et al.*, 2014). A recent stoichiometric analysis of this phenomenon (Anderson *et al.*, 2017) indicated that overall transfer efficiencies for detritus utilization by zooplankton may be very low, e.g. 1.45%, because of the low biomass of (nutritious) microbes present within the detrital matrix. This means that, when using this parameter value for trophic transfer, the predicted production of detritivorous copepods in the mesopelagic zone was only 0.16% of PP. As such, detritivorous copepods are only a minor source of food for mesopelagic fish. If the transfer efficiency is increased more than 15-fold to 0.23, a value used in previous models (Anderson and Tang, 2010; Giering *et al.*, 2014), the predicted share of detritivorous copepods in the diet of mesopelagic fish increases from 5% to 42% and predicted fish biomass increases from 2.4 to 4.6 Gt. Anderson *et al.* (2017) highlighted the need for more information on the physiological and ecological interactions between zooplankton, microbes and detritus. Our work here serves to re-emphasize that need.

The model was parameterized as a general representation of the flows of C between PP and the mesopelagic ecosystem between  $40^\circ\text{S}$  to  $40^\circ\text{N}$  in the world ocean. A simple approach is justified at this stage given the many uncertainties in our understanding of the mesopelagic ecosystem. The structure and function of marine ecosystems are in reality variable in space and time. For example, the export of sinking detritus as a fraction of PP is variable (Dunne *et al.*, 2005; Henson *et al.*, 2011; Siegel *et al.*, 2014) which will in turn mean that the relationship between mesopelagic fish biomass and PP is not necessarily linear. Likewise, the contribution of copepods to overall grazing of PP is also variable in space and time (Calbet, 2001). Recent studies of mesopelagic biogeography have defined as many as 33 biomes throughout the ocean (Proud *et al.*, 2017; Sutton *et al.*, 2017). These studies were, however, limited by the sparsity and spatio-temporally biased data sets available such that much work remains in order to derive biomes that are comprehensive and robust (Sutton *et al.*, 2017). As and when robust biomes are defined, it may then be possible to extend our model to investigate spatiotemporal variability in the dynamics of the mesopelagic ecosystem and the associated production of fish biomass. If



the model was parameterized beyond the latitudinal range 40°S to 40°N, a factor to consider is that high latitude, lipid-rich zooplankton undergo seasonal migrations and thereby transfer significant amounts of labile C to the mesopelagic zone via the “lipid pump” (Jónasdóttir *et al.*, 2015). Estimates of mesopelagic fish biomass at the global scale should take into consideration this C as an additional source of energy and nutrition to mesopelagic fish.

In conclusion, we used a flow analysis model to study C fluxes from PP to the mesopelagic ecosystem, giving a prediction for mesopelagic fish biomass of 2.4 Gt w.w. (between 40°S and 40°N in the world ocean). Defining the mesopelagic food web interactions in the model was problematic and many of the associated parameter values were poorly constrained. Our model analysis highlights how little is known about the physiological ecology of mesopelagic fish, trophic pathways within the mesopelagic food web, and how these link to PP in the surface ocean. A deeper understanding of these interacting factors is required before the potential for utilizing mesopelagic fish as a harvestable resource can be considered as a viable proposition.

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