LIMNOLOGY and OCEANOGRAPHY

Toward a better understanding of fish-based contribution to ocean carbon flux

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Abstract

Fishes are the dominant vertebrates in the ocean, yet we know little of their contribution to carbon export flux at regional to global scales. We synthesize the existing information on fish-based carbon flux in coastal and pelagic waters, identify gaps and challenges in measuring this flux and approaches to address them, and recommend research priorities. Based on our synthesis of passive (fecal pellet sinking) and active (migratory) flux of fishes, we estimated that fishes contribute an average ($\pm$ standard deviation) of about 16.1% ($\pm$ 13%) to total carbon flux out of the euphotic zone. Using the mean value of model-generated global carbon flux estimates, this equates to an annual flux of 1.5 ± 1.2 Pg C yr^{-1}. High variability in estimations of the fish-based contribution to total carbon flux among previous field studies and reported here highlight significant methodological variations and observational gaps in our present knowledge. Community-adopted methodological standards, improved and more frequent measurements of biomass and passive and active fluxes of fishes, and stronger linkages between observations and models will decrease uncertainty, increase our confidence in the estimation of fish-based carbon flux, and enable identification of controlling factors to account for spatial and temporal variability. Better constraints on this key component of the biological pump will provide a baseline for understanding how ongoing climate change and harvest will affect the role fishes play in carbon flux.

The "biological pump," the vertical transport of biologically generated dissolved or particulate organic matter from the surface to the ocean's interior, plays a key role in ocean biogeochemistry and modulates ocean ecosystem productivity and associated living marine resources (Ducklow et al. 2001; Fasham 2003; Siegel et al. 2016). In this process, carbon

dioxide (CO_2) is fixed into organic carbon by photosynthetic phytoplankton in the euphotic zone. This organic carbon is then passively (via sinking of particles), actively (via vertical migration of zooplankton and fish), or physically (via advective-diffusive transport) transported to deeper water (Ducklow et al. 2001) in either particulate or dissolved form. As particles sink below the euphotic zone, their carbon is respired and consumed by mesopelagic bacteria, zooplankton, and fishes. A small proportion of particulate matter produced at the surface reaches the seafloor (e.g., Lutz et al. 2002) where it can be utilized by benthic organisms. The depth and location at which organic carbon is transported and remineralized

determine how long the carbon is sequestered in the ocean (DeVries et al. 2012).

The contribution of fishes to downward, or export, carbon flux has not been specifically quantified in present-day carbon budgets, but the flux is likely significant due to the high abundance of epipelagic fishes on coastal shelves and in upwelling regions and the high biomass of mesopelagic fishes in the vast expanse of oligotrophic regions. To improve parameterization in, for example, regional and global ocean coupled biogeochemical general circulation models and fully coupled carbon-climate earth system models, it is critical to understand the key processes affecting the biological pump (Honjo et al. 2014; Siegel et al. 2016; Burd et al. 2017). This must include quantifying the amount of carbon that fishes contribute to vertical flux relative to that from other taxa and the environmental and biological influences of the processes that determine both the magnitude and efficiency of these fluxes. Without a baseline assessment of the role fishes play in downward carbon flux, we cannot yet quantitatively address important mechanistic questions like how changes in food quality or quantity, environmental stressors, and ongoing climate change might impact the rate or magnitude of fish-based carbon flux.

In this review, we synthesize existing research on fish-based carbon flux, identify the gaps and challenges in measuring this flux and approaches to resolve them, and recommend research priorities to address large gaps in understanding. In doing so, we provide a fish-focused contribution to research areas needed to reduce key uncertainties in current and future estimates of carbon export. Quantitative and process-level analyses of the role fishes play in carbon flux enable understanding the observed spatiotemporal variability and long-term changes in fish-mediated flux. Ultimately, this will lead to a more holistic understanding of food web regulation of carbon flux, which has implications for climate change mitigation, will help inform fisheries management, and can aid in environmental impact assessments related to exploration and extraction of seabed-related resources. However, societal, ecological, and economic impacts of the trade-offs and interdependencies between carbon flux and uses of fishes and other marine resources (cultural, nutritional, commercial, recreational, pharmaceutical and mineral) requires further exploration (Martin et al. 2016; Hidalgo and Browman 2019).

Contributions to the "biological pump"

Marine zooplankton and finfishes influence the biological carbon pump through several mechanisms (shown for a myctophid fish in Fig. 1): (1) in surface waters, they provide respired carbon dioxide (CO_2) and often limiting dissolved excretory products that can support both bacteria and phytoplankton growth (e.g., Zimmer et al. 2006; Steinberg and Landry 2017); (2) they contribute to passive, or gravitational,
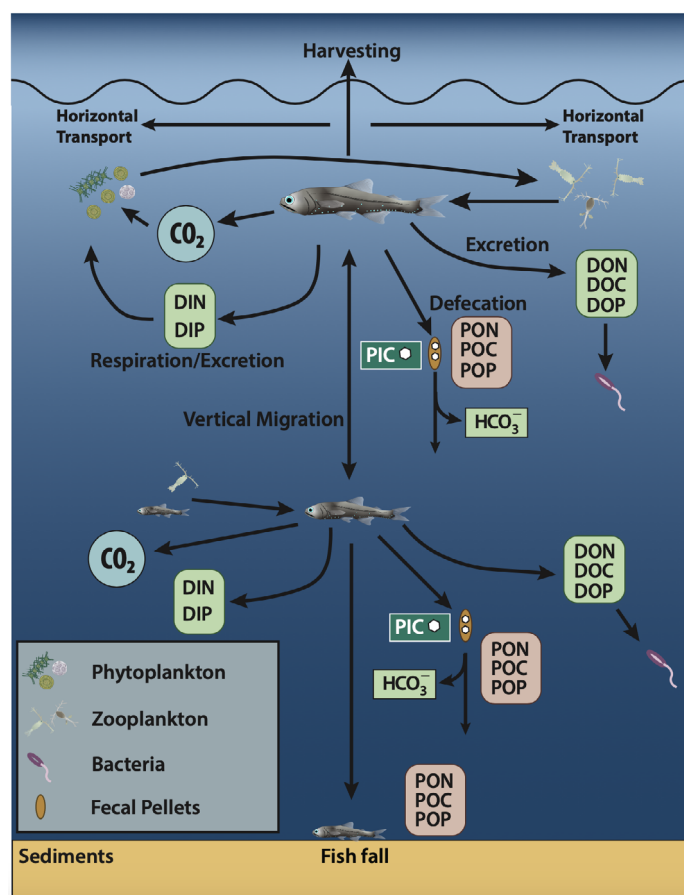

Fig. 1. Conceptual diagram highlighting the mechanisms by which fishes contribute to the biological carbon pump and nutrient cycling. Here, we use a diel vertically migrating midwater myctophid fish as a model organism. Arrows between different types of organisms infer predation from a prey item to a predator (arrow pointing to the predator; e.g., zooplankton feeding on phytoplankton in the upper water column, myctophids feeding on zooplankton in the upper water column, myctophid feeding on zooplankton and small fishes in mid-water). CO_2, carbon dioxide (excreted via gills); DIN, dissolved inorganic nitrogen (excreted via gills and kidney); DIP, dissolved inorganic phosphorus (excreted via gills and kidney); DON, dissolved organic nitrogen (excreted via gut fluids); DOC, dissolved organic carbon (excreted via gut fluids); DOP, dissolved organic phosphorus (excreted via gut fluids); PIC, particulate inorganic carbon (calcium carbonate; released via gut solids as precipitates in feces); HCO_3^-, bicarbonate (excreted via gut fluids); PON, particulate organic nitrogen (released via gut solids as feces); PON, particulate organic nitrogen (released via gut solids as feces); POC, particulate organic carbon (released via gut solids as feces); POP, particulate organic phosphorus (released via gut solids as feces). In most cases the abbreviations refer to complex mixtures of compounds that can be categorized as either dissolved (D) or particulate (P), and either inorganic (I) or organic (O) forms of the elements carbon (C), nitrogen (N), and phosphorous (P). Both CO_2 and HCO_3^- ions belong to the DIC category. However, because they have such important but opposite effects on acid–base chemistry of seawater, DIC has therefore been separated into these two compounds within this figure. While the route of released dissolved or particulate matter is described in the caption here, the arrows in the graphic do not differentiate where they are released from.

organic carbon flux by repackaging consumed prey into sinking fecal material that is rapidly transported from the surface to the deep ocean (Staresinic et al. 1983; Saba and Steinberg 2012; Wilson et al. 2013; Turner 2015). The term passive flux is typically reserved for epipelagic fishes, whereby the fecal pellets produced in the surface sink passively to deeper water; (3) diel vertically migrating (DVM) mesopelagic zooplankton and fishes feed in the surface layers at night, then return to deeper waters during the day, transporting carbon through excretion of respiratory CO_2 (Longhurst et al. 1990), dissolved organic carbon (DOC; Steinberg et al. 2000), and dissolved inorganic carbon (DIC; Wilson et al. 1996), as well as through fecal material (particulate organic carbon [POC]; Turner 2015) and precipitates of POC or PIC (Wilson et al. 2009; Perry et al. 2011). This flux is known as active, or migratory, flux. Although fecal pellets sink passively, if they are egested below the surface layer by DVM fishes, they are considered here as a component of active flux. Passive and active transports of carbon are dominant modes of flux in the biological pump; (4) fish mortality, either through the predation of DVM fishes at depth (active) or sinking of fish carcasses/fish parts (passive flux), can contribute an as yet unquantified amount to the biological pump. Lebrato et al. (2013) reviewed the available information for gelatinous zooplankton carcasses and Trueman et al. (2014) quantified these contributions in a regional context; (5) carbon is also likely transported horizontally by fishes, termed "horizontal transport," via daily movement cycles or seasonal migrations linked to spawning and ontogenetic cycles as well as by the transport of fishes in currents, eddies, and upwelling filaments. Upwelling filaments are a conduit for transporting zooplankton and larval fishes from the neritic coastal environment into offshore waters (Rodrıguez et al. 1999). Keister et al. (2009) estimated that upwelling filaments can move potentially $4–5 \times 10^4$ tons of zooplankton carbon offshore to the deep ocean and (6) fishes contribute to biogeochemical cycling of elements other than carbon through excretion of dissolved organic and inorganic nitrogen and phosphorus that can support bacteria and phytoplankton production and ultimately contribute to the biological pump through its entrance into microorganism-mediated carbon pathways.

Zooplankton setting the example for significant contributions to carbon flux

There is now considerable observational evidence to quantify the active and passive transports of carbon by zooplankton and their contributions to carbon flux (Turner 2015; Steinberg and Landry 2017). Mean values of active transport of respired CO_2 by vertically migrating zooplankton, compiled from studies in the North Atlantic and Pacific Oceans, are equivalent to 2–55% of POC export from the epipelagic zone measured by sediment traps (fig. 5b in Steinberg and Landry 2017). Sinking rates of small or low-mass fecal pellets of some zooplankton (e.g., copepods, euphausiids, doliolids, appendicularians, heteropods), as well as phytodetritus and marine snow, range from < 10 to hundreds of meters per day (Alldredge and Gotschalk 1988; Yoon et al. 2001; Turner 2015). Very large or high-mass fecal pellets of other zooplankton (e.g., salps, pteropods, chaetognaths) tend to sink at even faster rates (tens to thousands of meters per day) (Dilling and Alldredge 1993; Phillips et al. 2009). However, even with the many studies measuring zooplankton flux, there are still many uncertainties with respect to the factors that drive the spatio-temporal variability of zooplankton-mediated carbon flux. Given the overlap of mechanisms and processes, the large contribution of some zooplankton to carbon flux suggests fishes may also be a significant contributor.

Fish-based contributions to carbon flux

Despite the global ecological and economic significance of fishes, observations and process studies of their contributions to the ocean carbon cycle are lacking relative to phytoplankton, zooplankton and other taxa. To our knowledge, only five published studies have provided either direct measurements or estimation of passive carbon flux of fish fecal pellets (Bray et al. 1981; Staresinic et al. 1983; Angel 1985; Hopkins et al. 1996; Saba and Steinberg 2012), and fewer than 10 studies have estimated active transport via DVM fishes (Table 1). These few studies do suggest significant contributions of fishes to carbon flux. Sinking rates of fecal pellets produced by fishes reach well over thousands of meters per day (Bray et al. 1981; Robison and Bailey 1981; Staresinic et al. 1983; Saba and Steinberg 2012). Measured sinking rates of fecal matter produced by fishes were generally higher than those reported for euphausiids (16–862 m d^{-1}; Fowler and Small 1972; Youngbluth et al. 1989; Yoon et al. 2001) but within range of those reported for salps (300–2470 m d^{-1}; Bruland and Silver 1981; Madin 1982; Caron et al. 1989; Phillips et al. 2009). The feces produced by fishes in all five studies (cited above) were long cylinders that varied in diameter depending on the producing species. The cohesive nature of these fecal pellets suggests that, compared to amorphous particles, they are less susceptible to bacterial decomposition during rapid decent to the benthos. The combination of rapid sinking rates and slow decomposition in the water column facilitate fecal material from fishes produced near the surface to reach the benthos in < 1 d in most coastal systems (Saba and Steinberg 2012).

Fish-produced fecal material reaching the benthos is likely not limited to shallow coastal systems. Cylindrical fecal pellets believed to be produced by mesopelagic fishes were observed on several occasions in deep-moored sediment traps (3900 m depth) from the Sta. M long-term monitoring site off central California (Huffard et al. 2020). Anchovy (*Engraulis ringens*) fecal matter rich in organic carbon and nitrogen represented up to 17% of total carbon flux in sediment traps in the Peru upwelling system (Staresinic et al. 1983). Furthermore,

Table 1. Comparison of fish-based carbon export fluxes calculated in the literature. Where applicable, fish-based carbon export flux is compared to total sinking POC flux measured by sediment traps at depths near the base of the euphotic or epipelagic zone. These depths varied by study, but were typically between 100 and 200 m, except in Staresinic et al. (1983) where the base of the euphotic zone was located at depths 11–15 m and free drifting sediment traps were placed between 10 and 53 m. Active flux is flux associated with DVM fishes. For active flux, "fecal" (egestion of fecal pellets at depth) is the same as "gut flux" in some studies.

Species or group	Habitat (depth sampled)	Location	Temperature at sampling (°C)	Carbon flux type	Carbon export flux average (range) (mg C m^{-2} d^{-1})	% of gravitational POC flux out of epipelagic zone average (range) depth of flux (m)	References
Midwater fishes	Mesopelagic (to 1200 m)	Azores Islands	ND	POC (fecal/passive)	2.5[*]	ND	Angel (1985)
Blacksmith reef fish (*Chromis punctipinnus*)	Inshore reef, epipelagic (to 10 m)	Southern California	ND	POC (fecal/passive)	23 (ND-60)	ND	Bray et al. (1981)
Midwater fishes (100 + species)	Mesopelagic (to 1000 m)	Eastern Gulf of Mexico	ND	POC (fecal/passive)	ND (0.5–0.9)[†,‡]	ND	Hopkins et al. (1996)
Northern anchovy (*Engraulis mordax*)	Coastal, epipelagic (to 50 m)	Southern California	10–14.5	POC (fecal/passive)	31 (2–251)	ND	Saba and Steinberg (2012)
Peruvian anchovy (*Engraulis ringens*)	Coastal, epipelagic (to 50 m)	Peru upwelling	15	POC (fecal/passive)	32 (6.8–92)[§]	7.3 (0.7–17)[§] 10–53 m	Staresinic et al. (1983)
Midwater fishes (mostly myctophids)	Offshore, epipelagic (0–150 m)	Canary Islands	12	Active flux (respiratory)	2.7 (1.4–3.9)[¶]	23 (12–32)[¶] 150 m	Ariza et al. (2015)
Myctophids (*Electrona carlsbergi, Electrona antarctica, Gymnoscopelus braueri,* and others)	Mesopelagic (to 1000 m)	Scotia Sea, Southern Ocean	0.7–2.1	Active flux (respiratory)	0.18 (0.05–0.28)[**]	6.9[††] (1–47)[**] 200 m	Belcher et al. (2019)
Myctophids (*Gymnoscopelus* spp., *Electrona antarctica, Krefftichthys anderssoni,* and others)	Mesopelagic (to 500 m)	Scotia Sea, Southern Ocean	0.7–3.5	Active flux (respiratory)	0.61 (0.25–0.91)[**]	21.1[††] (3.1–143)[**] 200 m	Belcher et al. (2020)
Micronekton, dominated by myctophids	Mesopelagic (200–800 m)	Tropical and subtropical Atlantic Ocean	7.2–11.5	Active flux (respiratory)	0.43 (0.02–0.74)[‡‡]	3.6 (1.2–10.4)[‡‡] 150 m	Hernández-León et al. (2019)
Micronekton, dominated by myctophids	Mesopelagic (to 900 m)	South of Tasmania	ND	Active flux (mortality)	ND (3.1–11.1)[†]	ND	Williams and Koslow (1997)
Myctophids (various)	Upper Mesopelagic (to 160 m)	Western Equatorial Pacific	9.3	Active flux (respiratory, fecal)	ND (8.4–15.4)[¶]	20.7[††] (15.3–28.1)[¶] 160 m	Hidaka et al. (2001)

(Continues)

Table 1. Continued

Species or group	Habitat (depth sampled)	Location	Temperature at sampling (°C)	Carbon flux type	Carbon export flux average (range) (mg C m^{-2} d^{-1})	% of gravitational POC flux out of epipelagic zone average (range) depth of flux (m)	References
Midwater fishes (mostly myctophids)	Mesopelagic (to 500 m)	Northeast Pacific	7–13	Active flux (respiratory, fecal, mortality)	18.6 (8.0–30.8)[§§,¶¶] for VM; 31 (19–41)[§§,¶¶] for FME	22 (16–38)[§§,¶¶] for VM; 40 (24–53)[§§,¶¶] for FME; 150 m	Davison et al. (2013)
Myctophids (*Benthosema glaciale*, *Protomyctophum arcticum*, *Hygophum hygomii*, and others)	Mesopelagic (to 200 m)	Mid-Atlantic Ridge (North Azores)	4.2–15.6	Active flux (respiratory, excretory, fecal)	0.7 (0.04–2.8)[¶]	0.3[††] (0.01–7.5)[¶]; 200 m	Hudson et al. (2014)
Midwater fishes (various)	Mesopelagic (to 1000 m)	Northeast Atlantic	ND	Active flux (excretory, fecal, mortality)	ND (0.1–0.6)[†,***]	ND	Angel and Pugh (2000)

ND, not determined or reported.

* Estimated from DVM fish standing stock in and out of 500 m, an assumed daily ration of 10% body weight, 50% assimilation efficiency, and 5% fecal carbon content.

† Uncorrected for capture efficiency.

‡ Estimated from midwater fish standing stock and daily consumption rate assuming an egestion rate of 20% food intake.

§ Values reported here include only data where anchovy fecal pellets were present in sediment traps (in 12 out of 20 free-drifting sediment trap sampling deployments in fall of 1977 and fall of 1978).

¶ Assumes 14% capture efficiency.

** Maximum respiratory carbon flux as day-time net catches have not been corrected for capture efficiency.

†† Value estimated as the geometric mean from the ranges reported in the study.

‡‡ Assumes 50% capture efficiency.

§§ Assumes 14% capture efficiency for Matsuda–Oozeki–Hu trawls and an additional 6% capture efficiency for Isaacs-Kidd midwater trawls.

¶¶ Calculated from Davison et al. 2013 (table 9), comparing Vertical Migrant (VM) export and Fish-Mediated Export (FME; vertical migrant + nonmigrant export) to passive POC flux measured from sediment traps at 150 m).

*** Estimated from assuming total fish export flux is equivalent to 100% (fecal) plus 180% (excretory) plus 50% (mortality) of the fish standing stock (11.9–66 mg C m^{-2}).

Table 2. Estimates of modeled annual global carbon flux out of the euphotic zone (varies by study, but typically between 100 and 200 m) and mean fish-based carbon contribution. Mean fish-based carbon contribution (Pg C yr^{-1}) was determined using the calculated geometric mean of all means from applicable studies that estimated % of gravitational POC flux out of epipelagic zone from Table 1 (16.1%). Results of Coupled Model Intercomparison Project Phase 6 models for passive export at 100 m were taken from the Earth System Grid Federation (https://esgf-node.llnl.gov/projects/esgf-llnl/) (these models are the final seven listed in the table).

Model source	Model description	Depth of flux (m)	Global POC flux out of euphotic zone (Pg C yr^{-1})	Mean fish-based carbon contribution (Pg C yr^{-1})
Laws et al. (2000)	Semi-prognostic: EP[*]	NR	20.9	3.4
Laws et al. (2000)	Semi-prognostic: TE[†]	NR	12.9	2.1
Laws et al. (2000)	Semi-prognostic: PTE[‡]	NR	11.1	1.8
Bopp et al. (2001)	Coupled atmosphere–ocean general circulation: LGc[§]	100	13.1	2.1
Bopp et al. (2001)	Coupled atmosphere–ocean general circulation: LBc[¶]	100	11.1	1.8
Bopp et al. (2001)	Coupled atmosphere–ocean general circulation: AGc[**]	100	9.5	1.5
Moore et al. (2001*a,b*)	Prognostic ecosystem model[††]	NR	7.9	1.3
Gehlen et al. (2006)	Biogeochemical global circulation model: STD1[‡‡]	100	8.0	1.3
Gehlen et al. (2006)	Biogeochemical global circulation model: STD2[§§]	100	8.0	1.3
Gehlen et al. (2006)	Biogeochemical global circulation model: STD3[¶¶]	100	10.0	1.6
Gehlen et al. (2006)	Biogeochemical global circulation model: Aggregation/ disaggregation[***]	100	5.0	0.8
Gehlen et al. (2006)	Biogeochemical global circulation model: Ballast[†††]	100	11.0	1.8
Dunne et al. (2007)	Input data and flux algorithms[‡‡‡]	NR	9.6	1.5
Henson et al. (2011)	Thorium isotope tracer[§§§]	100	4.0	0.6
Siegel et al. (2014)	Satellite observations and food web models[¶¶¶]	40–110	5.9	0.9
Danabasoglu (2019)	Fully coupled community earth system model[****]	100	7.4	1.2
Danabasoglu (2019), Marsh et al. (2013)	Fully coupled community earth system model/whole atmosphere community climate model[††††]	100	7.4	1.2
Held et al. (2019)	Atmosphere–ocean coupled climate model[‡‡‡‡]	100	10.4	1.7
Mauritsen et al. (2019)	Earth system model[§§§§]	100	6.3	1.0
Sellar et al. (2019)	Earth system model[¶¶¶¶]	100	9.7	1.6
Boucher et al. (2020)	Atmosphere–ocean coupled climate model[*****]	100	7.3	1.2
Dunne et al. (2020)	Earth system model[†††††]	100	6.1	1.0
Arithmetic average			8.3	1.5

NR, not reported.

[*]Satellite-based estimate using the Eppley–Peterson (EP) model.

[†]Satellite-based estimate using a temperature-export ratio regression (TE).

[‡]Satellite-based estimate using a model relating export ratios to net primary productivity and temperature (PTE).

[§]Coupled atmospheric Laboratoire de Météorologie Dynamique/Océan Parallélisé Ice and geochemical Hamburg ocean carbon cycle models.

[¶]Coupled atmospheric Laboratoire de Météorologie Dynamique/Océan Parallélisé Ice and biogeochemical nutrient phytoplankton zooplankton and detritus-type models.

[**]Atmospheric Arpege weather forecast model coupled with geochemical Hamburg ocean carbon cycle model.

[††]Ecosystem model that consists of several compartments and tracks elements, including carbon, for the biota and detrital pools.

[‡‡]Standard (STD) Version 1 includes two size classes of phytoplankton and zooplankton, aggregation/disaggregations, and prescribed sinking speeds.

[§§]Standard Version 2 includes two size classes, no aggregation/disaggregation, and prescribed sinking speeds.

[¶¶]Standard Version 3 includes two size classes, aggregation/disaggregation, prescribed sinking speeds, and parameterization of zooplankton feeding.

[***]Full aggregation/disaggregation model includes a full spectrum of particle sizes, aggregation/disaggregation, prognostic sinking speeds.

[†††]Includes a mineral ballast parameterization, prognostic sinking speeds, and size class is ignored.

[‡‡‡]Satellite-based estimate with semiempirical algorithms calibrated to diverse field observations.

[§§§]Satellite-based estimate using thorium-derived export flux measurements.

[¶¶¶]Combination of satellite observations and a food web model.

[****]National Center for Atmospheric Research Community Earth System Model, Version 2.

[††††]National Center for Atmospheric Research Whole Atmosphere Community Climate Model variant of the Community Earth System Model, Version 2.

[‡‡‡‡]Geophysical Fluid Dynamics Laboratory atmosphere–ocean coupled climate model, Version 4.0.

[§§§§]Max Planck Institute for Meteorology Earth System Model, Version 1.2.

[¶¶¶¶]United Kingdom Earth System Model, Version 1.0, low atmosphere and ocean resolution.

[*****]Institut Pierre–Simon Laplace global climate model used in Coupled Model Intercomparison Project Phase 6, low resolution.

[†††††]Geophysical Fluid Dynamics Laboratory Earth System Model, Version 4.1.

estimated fecal pellet (POC) flux from the Northern anchovy (*Engraulis mordax* Girard) was comparable to those previously measured from euphausiids (Alldredge et al. 1987) and salps (Wiebe et al. 1979; Iseki 1981; Matsueda et al. 1986; Phillips et al. 2009) and was equal to, and sometimes exceeded, total POC flux measured previously by bottom-moored sediment traps deployed in the Santa Barbara Channel (Saba and Steinberg 2012).

Most studies reporting active transport focus on the abundant myctophids that constitute most of the migrating micronekton biomass (Hidaka et al. 2001; Davison et al. 2013; Hudson et al. 2014; Ariza et al. 2015; Belcher et al. 2019; Hernández-León et al. 2019; Belcher et al. 2020). Active transport by mesopelagic fishes (through respired, excreted, and egested fecal carbon and by deadfall) ranged between $\sim 0.01\%$ and 143% of sinking POC flux from the euphotic zone as measured by sediment traps (Fig. 1; reviewed in Table 1), which translate to an annual global carbon flux range of 0.0008–4 Pg C yr^{-1} (Table 2). As passive sinking of particles attenuates rapidly in the upper mesopelagic zone (Buesseler and Boyd 2009), active transport by myctophids becomes increasingly important at greater depths as a mechanism of carbon export, as some species vertically migrate 1000 m or more (Hudson et al. 2014; Ariza et al. 2015). These reported rates are highly variable, likely driven by differences in (1) estimated biomass; (2) the number of source components included; (3) the specific conversion factors, (4) rate: biomass ratios, and (5) the uncertainty in these various assumptions.

Davison et al. (2013) accounted for fish-based flux of carbon (also predominantly myctophids) due to respiration, defecation, and mortality. They calculated that fluxes of migratory fishes were equivalent to 15–17% of the POC flux in the region of study (Northeast Pacific). Angel (1985) estimated that, depending on the assimilation efficiency, active flux by myctophids near the Azores Islands could contribute the equivalent of 15–40% of the carbon flux measured by sediment traps. Belcher et al. (2019) measured respiratory flux of migratory myctophids in two areas that was equal to 10.5–56% of the sinking POC flux in the North Scotia Sea and 1.2–2.1% in the Georgia Basin. Hernández-León et al. (2019) also measured sinking POC flux and micronekton (dominantly myctophid and decapod) respiratory flux in the tropical and subtropical Atlantic that suggested a relatively low contribution of fishes (equal to 3.6% ± 3.4% of sinking POC flux) compared to a similar study (12–32%; Ariza et al. 2015). This difference was likely due to a higher estimation of fish migrant biomass in the Ariza et al. study (average 168 ± 61 mg C m^{-2}) compared to Hernández-León et al. (average 61.0 ± 51.7 mg C m^{-2}) caused by differences in the trawl capture efficiency adjustments used (14% vs. 50%). Applying a 20% trawl capture efficiency, the average migrant biomass in Hernández-León et al. (2019) of 152.6 ± 129.1 mg C m^{-2} becomes similar to that reported in Ariza et al. (2015; 168 mg C m^{-2}). With the revised biomass,

the respiratory flux of fishes to POC flux ratio was 4.2–26.0 mg C m^{-2} (average 8.9 ± 8.5), which is also similar to Ariza et al. (2015). Therefore, this comparison illustrates the importance of biomass estimation in quantifying the role of fishes in the biological carbon pump.

We used the reported values for fish-based carbon flux as a percent, along with other reported values of total global carbon flux to roughly estimate the annual global fish-based export of carbon out of the epipelagic zone. We first synthesized the available passive and active estimates of fish-based carbon export flux (Table 1, column: % of gravitational POC flux out of epipelagic zone) using mean values from the studies summarized in the table. For studies that reported minimum and maximum values only, we computed the geometric mean (*see* mean values marked with †† symbol in Table 1). The overall geometric mean (± standard deviation) of the estimated fish-based contribution to total carbon flux out of the euphotic zone (nine values; eight studies) was 16.1% ± 13% (range = 0.3–40%). Applying the mean of 16.1% to multiple estimates of model-generated values of annual global carbon flux (Table 2, column: global POC flux out of the euphotic zone in Pg C yr^{-1}) resulted in estimates of fish-based carbon contribution in Pg C yr^{-1} (Table 2, column: mean fish carbon contribution in Pg C yr^{-1}). The arithmetic mean (± standard deviation) contribution of fishes to total global carbon flux was about 1.5 ± 1.2 Pg C yr^{-1}. Our estimated mean contribution of fishes to total carbon flux (16.1%) is equivalent to the mean contribution estimated globally for DVM zooplankton (16% ± 4%; Archibald et al. 2019). However, fish-based carbon contribution estimates, from previous field studies and those resulting from our approach taken here, exhibit greater uncertainty compared to that modeled globally for zooplankton.

Understanding the biogeochemical significance of the export fluxes reported here near the base of the euphotic zone (100–200 m; Tables 1 and 2) requires further contextualization with respect to the depth this carbon reaches and the length of time those waters then remain separated from surface exchange. Carbon transported (passively or actively) below the euphotic zone to the base of the permanent thermocline is considered export flux. In this layer referred to as the mesopelagic zone or the "Twilight Zone," high rates of bacterial remineralization and zooplankton feeding rapidly reduce the magnitude of carbon flux and sequestration efficiency (Buesseler et al. 2007b). The depth of the permanent thermocline is regionally variable, ranging from 200 to 1000 m (Lampitt et al. 2008). Above this, exported carbon can be reintroduced to the surface through convective mixing processes (seasonal to decadal), and thus carbon remains in this layer on the order of years to tens of years. A small portion of the exported carbon reaches below the permanent thermocline, and becomes "sequestered" by entering deep ocean circulation for hundreds to thousands of years.

To further explore the potential sequestration of carbon, we conducted a ventilation timescale analysis from the two

Table 3. Estimates of modeled annual global carbon flux (Pg C yr^{-1}) out of the euphotic zone (100 m) and at 400 and 1000 m depths. Estimates were derived using Coupled Model Intercomparison Project Phase 6 models for passive export taken from the Earth System Grid Federation (https://esgf-node.llnl.gov/projects/esgf-llnl/) (these models are the same final seven listed in Table 2). Results from ventilation timescale analysis revealed the average time this exported material is sequestered at 100, 400, and 1000 m was 14, 104, and 352 yr, respectively.

Model source	Global POC flux out of euphotic zone at 100 m (Pg C yr^{-1})	Global POC flux at 400 m (Pg C yr^{-1})	Global POC flux at 1000 m (Pg C yr^{-1})
Danabasoglu (2019)	7.4	2.8	1.1
Danabasoglu (2019), Marsh et al. (2013)	7.4	2.7	1.1
Held et al. (2019)	10.4	4.2	1.2
Mauritsen et al. (2019)	6.3	2.1	0.96
Sellar et al. (2019)	9.7	1.5	0.34
Boucher et al. (2020)	7.3	2.7	1.5
Dunne et al. (2020)	6.1	2.3	0.84

Geophysical Fluid Dynamic Laboratory models in Table 2. The two models were the atmosphere–ocean coupled climate model (Version 4.0) of Held et al. (2019) and the earth system model (Version 4.1) of Dunne et al. (2020). We used model simulations to estimate the export (Pg C yr^{-1}) across timescales of carbon sequestration that take advantage of the ideal age tracer; this tracer resets to zero at the surface and acts as a ventilation clock below (Thiele and Sarmiento 1990). Here, we ignore the complex cycling of carbon on coastal shelves, where exported carbon can be derived from terrestrial sources and transported offshore, down the continental slope, and sequestered and/or buried (Hoffmann et al. 2011; Najjar et al. 2018). Based on this ventilation timescale analysis, we estimated that approximately two thirds of the sinking export past 100 m (Held et al. 2019 = 10.4 Pg C yr^{-1}, Dunne et al. 2020 = 6.1 Pg C yr^{-1}; Table 2) is sequestered for at least 10 yr (at a depth of $\sim$ 150 m) and one third sequestered for at least 50 yr (at a depth of $\sim$ 300 m). Additional analyses produced model-generated values of annual global carbon flux at 100, 400, and 1000 m depths (Table 3) and associated sequestration times of flux exported at these three depths. Of the POC flux out of the euphotic zone (past 100 m), 15–40% (mean = 34%) is exported beyond 400 m. Of the POC flux that reaches 400 m, 22–56% (mean = 38%) is exported below 1000 m. The export at depths of 100, 400, and 1000 m corresponded to sequestration times of 14, 104, and 352 yr, respectively.

Sequestration at depth can be facilitated by the high biomass of DVM fishes, specifically myctophids that can perform vertical migrations to the surface from depths of 400 to 1000 m (Hudson et al. 2014). Mean contribution of only mesopelagic DVM fishes to total carbon flux ranged from 0.3% to 40% (using eight of the nine mean values from Table 1; one value was specific to passive flux from epipelagic fish). Therefore, if we assume that all mesopelagic fishes migrate below 400 m and that all of the carbon is respired, excreted, and egested at these depths during the day, fish

contribution to carbon flux at 400 m could contribute up to 1.7 Pg C yr^{-1}. Importantly, this active flux-derived carbon would be sequestered for over 100 yr. Less information is available on DVM fishes that migrate to 1000 m or deeper due to difficulties in sampling at these depths, although observations have confirmed such deep migrations do occur (Badcock and Merrett 1976; Hudson et al. 2014; Ariza et al. 2015). Carbon released from fish migrating to these deeper depths would be sequestered for much longer (over 350 yr).

In addition to the role of fishes in the biological pump, fishes also influence the cycling of inorganic carbon (Wilson et al. 2009; Perry et al. 2011; Salter et al. 2019). Specifically, marine bony fishes continuously produce carbonates in their guts as a by-product of the osmoregulatory need to continuously drink seawater. The intestines of all marine teleosts secrete a great excess of HCO_3^- ions, resulting in a highly alkaline environment that then precipitates the ingested seawater calcium and magnesium in the form of a high magnesium calcite mineral (Wilson et al. 2009; Perry et al. 2011). Globally, marine teleosts were (conservatively) estimated to contribute up to 15% of total surface oceanic carbonate production, and up to 45% when more realistic assumptions about fish metabolism were used (Wilson et al. 2009). Specific to reef fishes in a shallow tropical environment, their gut carbonates contribute a substantial fraction (14%) of the carbonate sediments of The Bahamas. The global-scale significance of this fish-mediated inorganic carbon production lies in the rapid dissolution of sinking fish-produced carbonates in the open ocean. Such rapid dissolution explains the long-standing mystery of the alkalinity-depth profile in both the Atlantic and Pacific Oceans—that is, the seawater alkalinity increases at shallower depths more than expected based on our understanding of other biogenic sources of calcium carbonate (mainly calcite and aragonite) (Milliman et al. 1999; Wilson et al. 2009). In addition, when fishes are feeding, the inorganic carbonate mineral will add dense ballast to fecal pellets and thus

potentially accelerate the sinking of excreted organic carbon in the feces. Although much of the understanding of gut carbonate mineralogy and morphology has been conducted using shallow tropical (Wilson et al. 2009; Perry et al. 2011) and subtropical (Salter et al. 2012, 2017, 2018) reef fish, Salter et al. (2019) compared new data from temperate fish species and these previously studied reef species across a range of temperatures (10–27°C). They observed fairly consistent carbonate mineralogy and morphology at both the species and family levels across this wide thermal range.

We can also use the removal of fishes through harvesting to derive carbon fluxes out of the ocean to the atmosphere. Approximately 10% of fish biomass is carbon (Czamanski et al. 2011). Given this assumption, extraction of fishes may represent a flux of carbon that was fixed in the ocean, but is respired directly to the atmosphere at subannual timescales. As an example, the human extraction of wild and cultured fishes (i.e., the actual landed biomass) is 0.014 Pg C yr^{-1} (FAO 2019), and that extracted by seabirds is an additional 0.007 Pg C yr^{-1} (Brooke, M. D. L. 2004). If we further assume that most of these fishes are extracted from the shelf regions, and that the total air-sea flux of carbon on the shelves is approximately ~ 0.25 Pg C yr^{-1} (Cai et al. 2006; Laruelle et al. 2010), then such an extraction represents over 8% of the total air-sea carbon flux on the global continental shelf. A global analysis based on historical catches and fuel consumption examined the role of ocean fisheries in atmospheric CO_2 emissions, and concluded that these activities have released a minimum of 0.73 Gt CO_2 into the atmospheric since 1950 (Mariani et al. 2020). However, for context, other sources of animal protein contribute significantly more CO_2 emission equivalents (livestock = 7.1 Gt CO_2-equivalent yr^{-1}) than global fisheries (Gerber et al. 2013).

The passive and active downward transport of particulate and dissolved matter mediated by fishes are likely significant components of both organic and inorganic carbon flux in the ocean but the information is uncertain and incomplete. Even with the available information being from mostly short-term studies that exhibit high reported variability among specific locations, the evidence is suggestive of a larger role played by fishes in the carbon cycle than previously thought.

Current gaps and challenges in measuring fish-based carbon flux

Any estimate of the contributions of fishes to carbon flux requires two main inputs: the biomass of fishes present and the rate at which fish-associated carbon is transported into the deep ocean. Both of these variables are challenging to quantify. Biomass of fishes and their contributions to the biological pump are inevitably impacted by species composition, location, seasonality, temperature effects on metabolism, variation in the horizontal and vertical distribution of biomass and associated differences in feeding behavior between populations, and

biogeographic shifts in fish and their prey in response to rising ocean temperatures (e.g., Cheung et al. 2010; Pinsky et al. 2013; Proud et al. 2017).

Extrapolation of laboratory- or field-based carbon flux measurements, including fecal pellet production rates and biomass-specific metabolic or excretion rates, require biomass or abundance and composition data for scaling up the estimates (e.g., from local to regional to global scales). Exploratory analyses of the available laboratory and short-term field results can inform the needed resolution of taxonomy and life stages for the biomass and abundance estimates. Examples of possible resolutions include size classes, functional groups based on feeding or digestive physiology, and life history types representing major ocean biomes such as DVM fishes in oligotrophic or small forage fishes in coastal shelf regions. Such aggregations of species can then be used to filter the biomass data to enable sufficiently accurate estimation of carbon dynamics across the diverse species comprising a fish communities and food webs. In addition, extrapolations require knowledge and constraints on spatial (horizontal and vertical) distributions of fishes. This represents a difficult challenge in fisheries science, not only for coastal migratory species, but also for fishes in the mesopelagic whereby recent studies identified several biogeographic ecoregions within the global mesopelagic realm (Proud et al. 2017; Sutton et al. 2017).

Biomass of fishes

A challenge for all carbon flux estimation is the necessity of knowing the biomass or other abundance metric of the fish pool in absolute terms. This is a major determinant of extrapolations of carbon-related rates, and conversely, is also needed for interpreting metabolic (oxygen consumption or respiration) rates from observationally based carbon flux estimation. Mobile organisms like fishes are notoriously difficult to sample in a manner that allows for estimation of their absolute biomass (Fraser et al. 2007; Jurvelius et al. 2011). Fishes exhibit behavior that results in gear selectivity or avoidance (small organisms pass through the mesh; some organisms avoid the gear). Their distributions vary by season and horizontally and vertically, and they often show patchiness on multiple spatial scales. Thus, most monitoring of fish biomass yields relative indices of abundance to normalize these biases and enable spatial and temporal comparisons (Hilborn and Walters 2013).

Biomass of fishes can be estimated using several different approaches, but all are subject to considerable uncertainty. Commonly used approaches are to: (1) scale-up areal density catch data from surveys to absolute units of biomass or abundance; (2) start with measurements of primary production and an estimated trophic transfer efficiency of energy/carbon and track biomass through the food chain; (3) apply size-based relationships and functional types to estimate the relative proportions of fishes at different trophic levels that can be applied to disaggregate lumped biomass estimates; and (4) borrow results from fisheries stock assessments that often report

annual population biomasses, although rarely distributed in space. These approaches can incorporate empirical data or modeling or both. All of these approaches directly apply to restricted spatial areas dictated by the data and how it was generated. A next step for all approaches is to scale-up the biomass and abundance values to the geographic area of interest (regional to global) for predicting carbon fluxes. Especially challenging is the necessity of having vertical resolution of the extrapolated values to enable accurate downward flux predictions. Mismatches are inevitable; for example, the survey data and stock assessment approaches are often limited in spatial resolution, the measured primary production values often vary on fine temporal and spatial scales, and species composition of fishes is highly specific to fine-scale availability of habitats within regions.

Much of the stock assessment data that inform fisheries management rely on relative indices, such as catch-per-unit-effort, which permit modeling of trends and indirectly derives absolute stock size (biomass). Absolute biomass can be estimated by combining catch data and harvest efficiency with population models that use growth, mortality, and reproduction to infer the biomass that would support the harvest estimated from catch; the relative indices are used to tune the temporal and spatial dynamics of the population model. Thus, much of these data focus on harvested species, specifically monitoring to provide the relative indices, on documented catch data, and on process studies to provide the growth, mortality, and reproduction rates. Because of higher data availability for many commercially and recreationally important species, these approaches to estimating biomass of fishes are suitable to apply in localized coastal shelf systems. However, the approaches for estimating this biomass contain uncertainties that become amplified when results are scaled regionally or globally for the estimation of carbon export.

For less well-studied species, particularly mesopelagic fishes in open ocean systems that are a focus of carbon flux estimation, there remain severe data limitations. Mesopelagic fishes dominate global fish biomass (Irigoien et al. 2014; Koslow et al. 2014). Direct biomass estimation of mesopelagic fishes using trawls is, at present, the most important bias precluding robust assessment of their role in the biological carbon pump. These biases are mostly due to escape of fishes from the front of the net (*see* Kaartvedt et al. 2012). Subsequently, trawl-based biomass estimates of mesopelagic fishes may be dramatically underestimated (e.g., Koslow et al. 1997; Kloser et al. 2009) unless they are corrected using estimates of trawl capture efficiency. Capture efficiency of trawls is based on several assumptions and the available studies indicate low and variable efficiencies depending on gear type, net dimension, trawl speed, and morphology. Capture efficiency was determined to be 14% for the Young Gadoic Pelagic Trawl (mouth opening 105 m^2; Koslow et al. 1997), and Davison (2011) applied different capture efficiencies for different organisms (14% for gas-bearing organisms, and 38% for nongas bearing

animals) for the smaller (5 m^2) Matsuda-Oozeki-Hu trawl (Oozeki et al. 2004). In addition, in comparing three framed midwater trawls (4, 12.3, and 16 m^2 mouth opening), Itaya et al. (2007) found capture efficiency to diminish linearly with the fish body length as a result of better swimming ability of larger fishes. Therefore, Davison et al. (2015*a*) used differential capture efficiencies for different organisms (100% for Cyclothones, 50% for other fishes < 3 cm, and 10% for fishes > 3 cm), and Davison et al. (2015*b*) also assumed a decreasing capture efficiency with increasing standard length.

Acoustic approaches show promise for estimating mesopelagic biomass (Irigoien et al. 2014). Recent acoustic-based biomass estimates of mesopelagic fishes are at least an order of magnitude higher than previous estimates from traditional trawl-based sampling. However, acoustic biomass estimates of mesopelagic fishes still range substantially from 1 to 20 Gt (Irigoien et al. 2014; Proud et al. 2019). While acoustic methods can provide synoptic views of biomass, they also have limitations, including nonlinear conversions of scattering strength to fish body weight and variability in signals due to aggregation of individuals (Davison et al. 2015*b*). Acoustic sampling may also miss biomass of fishes without swim-bladders (Dornan et al. 2019) or promote serious errors differentiating between, for example, mesopelagic siphonophores and fishes (Proud et al. 2019).

Emerging technologies developed for visual detection of fishes, such as video systems, remain challenged due to behavior of fishes (e.g., avoidance) in response to video systems and lights, making it difficult to produce representative deep-sea images. The use of infrared or even red lights could facilitate image capture (Widder et al. 2005) compared to white lights, but they may reduce image quality for species identification (Birt et al. 2019) and their limited penetration through the water precludes sampling large volumes as required with these relatively large organisms. Obtaining pictures of dark animals against a dark mesopelagic background is also challenging. However, a newly developed autonomous underwater vehicle, the "Mesobot," has the capability to modify red and white light intensity and control buoyancy allowing it to track targeted midwater organisms through the water column while capturing still images and video (Yoerger et al. 2018).

Multispecies, community-level, and food web models offer alternative to stock assessment or other field-based approaches for generating estimates of absolute biomass and fluxes of fishes. Regional and global models have been developed that generate biomass estimates of fishes, often either annually or seasonally. The spatial resolution of these models varies greatly, including models that represent one single well-mixed box, a water column with layers (1D vertical), a horizontal grid (for a layer like pelagic or vertically-mixed), and fully resolved 3D grids borrowed from hydrodynamics versions. Model-based biomass estimation of fishes has advantages in that one is truly dealing with absolute biomass (i.e., no gear

selectivity issues) for the spatial domain of interest (i.e., not limited to extrapolating from monitoring locations). However, the uncertainty in these estimates is both unknown and likely high and not uniformly distributed across regions, time periods or functional groups. Model-based biomass estimates are comparable but often rely on parameter values with unknown uncertainty, borrowed across species and locations, and dependent on the skill of the models earlier in the chain of coupled calculations (e.g., physics, nutrient-phytoplankton-zooplankton). Thus, when needing absolute biomass values, there is a trade-off between well-studied, managed species that have estimates but may not be the dominant source for global carbon fluxes vs. less studied but more broadly representative species that pose challenges for biomass estimation but enable better scaling of carbon flux to the system level. Spanning the gap between these two will require a broadening of observational and laboratory studies to include more representative species.

Coupled circulation-biogeochemistry models provide an overall context for characterization of stocks and fluxes constrained by mass and energy balances, but the mechanisms are only coarsely defined for fishes. This class of models typically limit ecosystem representation to lower trophic levels up to mesozooplankton and have been applied both with ocean models forced by historical atmospheric reanalysis (e.g., Stock et al. 2014) and fully coupled carbon-climate earth system models for future projections (Bopp et al. 2013). Results from these models are frequently used as inputs to ecosystem models that explicitly include fishes (e.g., Woodworth-Jefcoats et al. 2013; Christensen et al. 2015). A recent trait-based mechanistic model used allometric relationships between three fish functional types (forage, large pelagic, demersal) and their prey and coupled it to an earth system model that can be used to estimate global biomass of fishes (Petrik et al. 2019). Data-driven food web models, such as Ecopath with Ecosim (EwE) and Atlantis, represent fishes in more detail but are mostly applied at the water body or regional scale. Building on the foundational ecosystem modeling of Polovina (1984; Ecopath), the pioneering work of Pauly et al. (2000) introduced highly structured and energetically balanced food web/ecosystem modeling that provided a data-based framework to constrain these complex food webs. Guiet et al. (2016) provide a summary of efforts to represent size, community structure, and life history in ecosystem models. While uncertainties tend to be somewhat smaller for data-driven modeling frameworks like EwE and Atlantis and larger for trait driven including size-based models (e.g., Blanchard et al. 2012), the data-driven models are more restricted to well-observed areas while the trait-based approaches provide a means for global extrapolation. Therefore, existing independent modeling approaches exhibit specific limitations that make it difficult to comprehensively quantify biomass of fishes.

While there are many examples of regional models that could be used to generate biomass of fishes, models that are sufficient to generate biomass of mesopelagic fishes are more limited and global versions for mesopelagic fishes are even less common. Regional models may be difficult to combine due to the differences in the models used and the spatial and temporal aspects of the regional simulations that provide the biomass estimates. Global versions provide for consistent estimation across regions but seldom have the spatial and taxonomic resolution for generating biomass at a finer level than very coarse functional groups.

Passive flux

To estimate the contribution of fish-produced fecal pellets to organic carbon flux on a regional or global scale, we need to determine the following components: (1) the abundance or biomass of fishes in the region; (2) fecal pellet production rate of fishes (per fish or unit biomass per day); (3) fecal pellet sinking rates; and (4) fecal organic and inorganic carbon content. Few field studies have directly measured both fish fecal pellet sinking rates and organic carbon content (Bray et al. 1981; Staresinic et al. 1983; Saba and Steinberg 2012), and little or no published data exist from laboratory-based studies to determine values for most of these parameters. In particular, measurement of fecal production rates is important to obtain but very difficult to determine in the field. In addition, measurements of in situ abundance of fecal pellets of fishes and their associated particulate organic carbon flux are lacking, reflecting the difficulty of adequately combining these measurements to estimate the export of these particles. Deriving fecal pellet fluxes of fishes using traditional methods (i.e., thorium disequilibrium technique, sediment traps) is further challenged by both the thorium concentration differences between migrating fishes and sinking particles and the high mobility and schooling of fish that lead to spatial heterogeneity or "patchiness" in fecal pellet production in surface waters (Buesseler et al. 2007a). Sediment traps clearly have difficulty adequately sampling fish-produced fecal material, as evidenced by comparing calculated fish fecal flux in situ (using fecal pellet abundance, carbon content, and sinking rates) to POC flux measured by sediment traps. For instance, the calculated maximum downward flux of fecal POC from a large school of Northern anchovy (*E. mordax* Girard; 251 mg C m^{-2} d^{-1}; Saba and Steinberg 2012) sometimes exceeded previous short-term measurements of sediment trap POC flux in the same region. Reported POC fluxes were similar or less than the 251 mg C m^{-2} d^{-1} estimated for Northern anchovy: 20–200 mg C m^{-2} d^{-1} at 540 m (Thunell 1998); 50–300 mg C m^{-2} d^{-1} at 470 m (Shipe et al. 2002); 7–108 mg C m^{-2} d^{-1} at 100 m (Goldthwait and Alldredge 2006). In addition, of the five studies that have either estimated or directly measured passive carbon flux of fecal pellets of fishes, only one study estimated this fish contribution to total carbon flux (Staresinic et al. 1983; Table 1). This underscores the need to incorporate approaches that measure total carbon flux simultaneously with field estimates of the passive flux of fish pellets.

Furthermore, while characteristics such as fecal pellet shape and cohesiveness were consistent in the few fish species studied so far (blacksmith reef fish, Bray et al. 1981; Peruvian anchovy, Staresinic et al. 1983; Northern anchovy, Saba and Steinberg 2012), there is a clear need for evaluation across a broader range of ecologically relevant species. Comparison with zooplankton data highlights the importance of broadening this research in fishes. High variation in observed sinking velocities and carbon content of zooplankton fecal pellets results from variability in diet, feeding rates, assimilation efficiency, size, and species, and these differences have been associated with a wide range in relative contribution of vertical carbon flux over space and time (reviewed in Turner 2015). POC, PON, and POC : PON ratios of fecal pellets produced in just one location by one fish species, the Northern anchovy, were highly variable (POC = 15–31 μg C pellet^{-1}; PON = 2–6 μg N pellet^{-1}; POC : PON$_{molar}$ = 7–14; Saba and Steinberg 2012). This variability is similar to that found for composition of fecal pellets produced by Antarctic krill (*Euphausia superba*), which was attributed to differences in digestion time, absorption efficiency, and pellet diameter and density ultimately linked to diet (Atkinson et al. 2012). Differences in these krill fecal pellet characteristics significantly impacted sinking rates, whereby pellets containing less organic carbon were produced at a slower rate, were denser, and exhibited faster sinking rates (Atkinson et al. 2012). Studies to identify drivers of POC and PON content and ratios of POC : PON in fish fecal matter, and how these may affect sinking rates, have not yet been conducted. The lack of knowledge on fish fecal matter sinking rates and carbon content that are species-specific or pellet size-, shape-, mass-, or density-dependent, could lead to either overestimation or underestimation when extrapolating to determine community-based or regional to global carbon sequestration potential.

We also need to address knowledge gaps on the production of inorganic carbon by fishes, specifically the calcium carbonate content of fecal pellets, the carbonate mineral type(s) involved, and dissolution rate as the material sinks. Dissolution during sinking is of particular interest because of its influence on the vertical transport of the organic carbon in these pellets that is referred to as the "ballast hypothesis" (Armstrong et al. 2001; Klaas and Archer 2002). Hence, there is an unexplored, but possibly important and dynamic, interaction between the PIC and POC portions (i.e., POC : PIC) of fecal pellets of fishes and their contribution to carbon fluxes. Data that now cover 82 species from 45 families reveal a diverse range of CaCO$_3$ mineral types, including low-Mg calcite, aragonite, and highly soluble amorphous Ca–Mg carbonate, which vary greatly in their solubility (Brečević and Nielsen 1989; Perry et al. 2011; Salter et al. 2012, 2017, 2018, 2019; Foran et al. 2013). Most published data are only relevant to shallow tropical, subtropic, or temperate regions, and existing family-level data sets represent less than 10% of the global fish biomass, leaving the vast majority of fish species

unaccounted for in attempts to model inorganic carbon fluxes on a global scale. While carbonate mineralogy and morphology has been fairly consistent at the family level in these previous studies (Salter et al. 2019), a significant challenge is to identify suitable species and measurement approaches that can examine if these characteristics remain consistent across communities such as mesopelagic fishes.

Another important factor is the role of feeding and diet of the fish species of interest. Most previous studies on fish carbonate production (e.g., Wilson et al. 2009; Perry et al. 2011) used starved fish to standardize conditions across species and to allow collection of "clean" calcium carbonate material. Diets of fishes can be calcium-rich (fishes with calcium phosphate bones or invertebrates with CaCO$_3$ shells), but most fishes have a highly acidic stomach that dissolves such dietary minerals and releases free Ca^{2+} ions into the alkaline intestines where they precipitate as newly formed carbonate minerals. A laboratory study on the carnivorous European seabass showed that fed fish can produce and excrete 10 times more CaCO$_3$ than starved fish (S. Newbatt and R. W. Wilson unpubl.), suggesting that global carbonate production may be substantially higher than previously estimated. It also highlights the need for more research on the mineralogy and solubility of carbonates produced by fishes feeding on their natural diets in the wild, rather than during starvation, and the need for measurements of the PIC : POC ratio within their fecal pellets and how this influences their sinking rate of their pellets.

More details on excretory behavior of fishes will also be important, specifically when and where excretory material is released from the gut. The diel vertical migration of many myctophid species raises two further important uncertainties: (1) effects of temperature and pressure changes with depth on the production and excretion of intestinal carbonates; and (2) influence on the release of carbonates of feeding near the surface that releases rapidly dissolving minerals at night that were produced during the day while digesting at depth. This diel vertical migration creates a novel "upward alkalinity pump" (Roberts et al. 2017). The limited information on solubility of fish-derived carbonate minerals suggests that high-Mg calcite has a solubility that is approximately double that of aragonite (Woosley et al. 2012). However, given the expanding range of observed carbonate mineralogies of fishes (Salter et al. 2012, 2014, 2017, 2018, 2019), more quantitative data on solubility and dissolution rates for these different types of carbonate are needed.

Active flux

Sediment traps do not sample active flux, and approaches to measure active flux must make several assumptions about the energy budget components of the fish, including size, metabolic rate, swimming speed, and growth rate. All of these terms in the fish energy budget vary among individuals and species and are influenced by local environmental conditions. Active flux is estimated from migrant biomass and physiological rates of fishes

(respiration, excretion, egestion, and mortality) at their residence depth. Biomass of migrant fishes is obtained from catches performed at night in the epipelagic layer (Hernández-León et al. 2019), after which organisms are classified and weighed.

Respiration is commonly estimated and compared in terms of oxygen consumption rate. A first approach to assess respiration rates is the use of empirical allometric relationships relating oxygen consumption rates to temperature and body weight. These allometric relationships are generally well-known (e.g., Beamish 1964) and recent bathymetric models relating respiration, temperature, body weight, and depth (Ikeda 2016) can be used to estimate fish respiration. Measurement of metabolic rates in fish can be measured upon collection with nets equipped with closing cod-ends (*see* Childress et al. 1978) and incubation in an intermittent flow respirometer (Treberg et al. 2016). These measurements are currently performed taking into account the swimming activity and nutritional status of organisms (see Childress and Thuesen 1992). Mesopelagic fishes present a specific challenge because they are difficult to collect and incubate (*see* Robison and Bailey 1981); thus, other approaches are used to assess respiration. The most widely used is the measurement of the enzymatic activity of the electron transfer system in the cell (Packard 1971). Using this methodology, Ikeda (1989, 1996) obtained a relationship between body weight and respiration in myctophid and sternoptychid fishes using standard relationships between electron transfer system and respiration. Ikeda used two alternative methods to estimate respiration: calculated from simultaneous respiration and electron transfer system measurements on tropical reef fish (Ikeda 1989) or using a theoretical respiration: electron transfer system ratio of two based on previous comparative measurements of respiration and electron transfer system on zooplankton and fish (Ikeda 1996). In a recent study, Belcher et al. (2020) compared electron transfer system measurements with allometrically estimated rates for respiration of mesopelagic fishes in contrasting environments of the Benguela Current and Southern Ocean. However, calibration of the enzymatic activity and respiration is still lacking, and an effort should be made to obtain reliable estimates of the ratio of respiration rates to electron transfer system values to allow comparability of respiration rate across methods.

Metabolic rates of fishes are commonly reported as standard metabolic rate, which is defined as the minimum oxygen requirement required to sustain tissue function. However, energy consuming factors such as digestion (specific dynamic action) and activity elevate respiration above standard metabolism. Total or field-measured metabolic rates are difficult to determine in natural conditions (Treberg et al. 2016), but recent approaches based on isotopic proxies for field metabolic rate and considerations of range limits of species in the context of oxygen supply and demand ratios suggest that sustained field metabolic rates of marine fishes may be more than three times higher than standard metabolic rate (Chung et al. 2019*b*; Deutsch et al. 2020). Energy consuming processes

may be unevenly distributed in terms of vertical position in the water column or season and may not scale with body size and temperature in the same way as thermodynamically driven variation in standard metabolic rate. Field metabolic rates are therefore the most relevant measure of respiration for estimating carbon flux and production.

Carcasses/mortality contributions to flux

Natural senescence in fishes is presumed to be minimal with only scraps of fish, generated by predation, sinking through the water column (Britton and Morton 1994). In areas of high surface productivity, however, carcasses of fishes can provide an important localized source of carbon to benthic communities. For instance, supply in one area of the Angola continental margin was estimated at 0.4 mg C m^{-2} d^{-1} (equivalent to 4% of the estimated particulate carbon flux) (Higgs et al. 2014). Data on natural mortality of fishes are limited and difficult to observe in the field, but telemetry (Bird et al. 2017; Villegas-Ríos et al. 2020) or size-dependent relationships with mortality (Lorenzen 1996; Sogard 1997) may offer insights. For example, over a period of 7 yr, natural senescence was observed in 17% of cod (*Gadus morhua*) tagged with acoustic transmitters in a coastal marine reserve where fishing is prohibited (Villegas-Ríos et al. 2020). The practice of discarding unwanted catch by fishery vessels has increased carcass-bound carbon fluxes worldwide (Ramsay et al. 1997); about 9.1 million tonnes were discarded annually between 2010 and 2014 (Pérez Roda et al. 2019), which could have contributed approximately 0.91 million tonnes C yr^{-1} from bycatch alone.

Interception of vertically migrating fishes by predators at depth may further contribute to fish-based carbon export, particularly at continental margins where productivity is enhanced through upwelling. Trueman et al. (2014) combined fish biomass estimates, categorized by their feeding strategy, with stable isotope approaches to discriminate between pelagic and benthic diet sources. Isotope-based methods estimate that benthopelagic fishes living at water depths between 500 and 1800 m on the UK–Irish continental slope mediate a vertical carbon flux from surface, mixed waters to depths below 1000 m of about 1×10^6 tonnes of CO_2 yr^{-1}.

Determining relative contributions of flux

Few studies assess the relative carbon flux contributions of the source of carbon released (respired CO_2, egested POC, excreted DOC, DIC, or PIC) or the different modes of transport (active, passive, carcass) due to the logistical challenges of fish collection and direct measurements of rates. Hidaka et al. (2001) determined that myctophid gut (fecal) flux was about 9.6% that of respiratory flux. Recent experiments using a model marine mesopelagic zooplanktivorous fish (marine medaka) demonstrated these fish can transform substantial proportions of their ingested food and released body carbon (L. Zhou pers. comm.) into DOC. Excretion of DOC accounted for 39–42% of the body carbon released, compared to 40–45%

via respiration of CO_2 and 16–18% as particulate carbon (L. Zhou pers. comm.). Most other studies reporting active flux with multiple components (respiratory, fecal, excretory, mortality) assumed relationships between these variables based on zooplankton or other taxa (e.g., Davison et al. 2013; Hudson et al. 2014) that might not be applicable to fishes. To obtain more robust estimates of fish-based carbon flux, it is imperative that we obtain more fish-based physiological data to better quantify these relationships and improve estimates of the relative contributions of passive and active pathways.

Studies that include simultaneous measurements of zooplankton- and fish-mediated fluxes are extremely valuable for exploring the controls on the relative importance of fish-mediated carbon transport compared to other sources. Sediment trap studies show that zooplankton fecal pellets can contribute from 0% to 100% of sinking POC (*see* Turner 2015). Gelatinous salps, which are also patchy and comparable in size to some fishes, produce large, rapidly sinking fecal pellets that can contribute substantially to carbon export (e.g., Phillips et al. 2009; Wilson et al. 2013; Stone and Steinberg 2016). Indeed, fecal pellet sinking rates are similar between salps (200–1400 m d^{-1}) and smaller fishes such as the Peruvian and Northern anchovies that have pellet sinking speeds of 691–1987 and 485–1370 m d^{-1}, respectively (Staresinic et al. 1983; Phillips et al. 2009; Saba and Steinberg 2012). Comparing the fluxes of fish vs. zooplankton fecal pellets may be problematic using sediment traps, which are likely to underestimate fish-produced fecal pellet flux due to the rarity of large-size pellets and patchiness of distributions of fishes relative to zooplankton (Saba and Steinberg 2012; Davison et al. 2013).

The respiratory fluxes of DVM zooplankton reviewed in Steinberg and Landry (2017) were typically higher (up to $\sim$ 30 mg C m^{-2} d^{-1}) than those reported for myctophid fishes (Table 1). Ariza et al. (2015) used electron transfer system and biomass to calculate active respiratory flux from both fishes (predominantly myctophids) and zooplankton in the Canary Islands region and compared it to sediment trap POC flux. Zooplankton respiratory flux accounted for 10–37% of the sinking POC flux, which was comparable to that of fishes (12–32%) (Fig. 2), but fluxes due to excretion, defecation, and mortality at depth were not considered. Hidaka et al. (2001) conducted a series of net tows during a sediment trap deployment in the Western Equatorial Pacific, and compared relative zooplankton, fishes, and other micronekton (e.g., decapods) fluxes to total POC flux out of the upper 160 m. They derived three components of active flux (respiratory, mortality, and gut flux) using various previously published rates, Q_{10} adjustments, and relationships to dry weight and ingestion. The contribution of fish-based respiratory flux to total POC flux was estimated at between 15% and 28% of the total POC flux, while zooplankton contributed between 18% and 43% (Fig. 2). However, in a study located in tropical and subtropical Atlantic, fishes contributed comparatively less to total POC flux (3.6 $\pm$ 3.4%) relative to zooplankton (61.5 $\pm$ 56.9%) and other micronekton
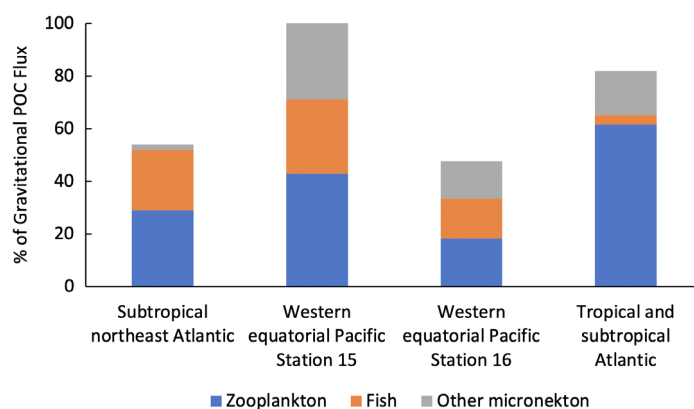

Fig. 2. Comparisons of zooplankton-, fish-, and other micronekton-mediated mean flux equal to % of gravitational (sinking) particulate organic carbon (POC) flux as measured by sediment traps in different oceanic regions, or stations within a region. Subtropical Northeast Atlantic (Canary Islands; Ariza et al. 2015, Table 3, includes only respiratory flux); Western equatorial Pacific (Stas. 15 and 16 in Hidaka et al. 2001, Tables 3 and 4, includes respiratory and gut, or fecal, flux); tropical and subtropical Atlantic (transect from Salvador de Bahía (Brazil) to the Canary Islands (Spain); Hernández-León et al. 2019; includes only respiratory flux).

(decapods, 16.9 $\pm$ 19.0%) (Hernández-León et al. 2019) (Fig. 2). This could be due to either differences in sampling gear capture efficiencies for fishes or due to the presence of an oxygen minimum zone along the sampling transect that was characterized by high abundances of decapods relative to fishes.

A fully coupled modeling framework was used by Aumont et al. (2018) to predict active flux of zooplankton and micronekton. They made a first assessment of active flux at the global scale and also considered fishes as drivers of carbon export. They found higher active flux coinciding with areas of higher primary production in agreement with the finding of Hernández-León et al. (2019) of a close relationship between primary production and total (zooplankton and micronekton) active flux at the basin scale in the Atlantic Ocean. Hernández-León et al. (2019) also found a significant relationship between primary production and passive flux but with remarkable lower slope compared to active flux. These differences suggested an increase in the ratio of active to passive flux in areas of higher primary production as observed in the model results by Aumont et al. (2018). However, Davison et al. (2013) found this ratio to be low in upwelling zones and increasing offshore, although at a quite different scale (global vs. regional). Differences in biomass between the coastal upwelling core or between values of metabolism (constant or varying depending on prey availability) could cause these differences and illustrate how modeling choices can lead to different results.

Overcoming challenges in measuring fish-based carbon flux

In the absence of direct observations of accurate biomass of fishes and/or the rate of production, sinking and

remineralization of fish-derived carbon, indirect estimates can be drawn from ecological theory or modeling approaches, but such approaches typically require physiological metabolic data that may be missing for key fish groups. An analysis of how to group species (or functional groups) using available physiological, diet, and habitat usage information would enable a functional grouping scheme designed for the specific question of predicting carbon fluxes from imperfect biomass data.

Biomass of fishes
Sampling issues

To address limitations in sampling approaches in the meso-pelagic, Davison et al. (2015*b*) combined acoustic sampling with traditional sampling (trawls) to estimate biomass of mesopelagic species in the California Current Ecosystem, one of the few locations that has a long-term sampling program for mesopelagic fishes (Koslow et al. 2014). Using this approach, biomass estimates of mesopelagic fishes (25–37 g m^{-2}) were comparable to those of epipelagic forage fishes (Davison et al. 2015*b*). Although this approach may not be economically or logistically feasible in all locations, employing this dual measurement approach in key regions (e.g., representative ecosystems or biogeographic ecoregions; Proud et al. 2017; Sutton et al. 2017) would improve estimates of trawl capture efficiency and acoustic modeling of backscatter. A dual method approach would enable more accurate biomass estimation from future monitoring efforts.

Modeling approaches

Coupled circulation-biogeochemistry models provide a pathway to estimate carbon biomass and fluxes, including those due to fishes, when the models are also coupled to ecosystem models that explicitly include difference types of fishes. More data on the conditions under which individual functional types dominate and better constraints on the behavior and traits of these functional groupings under varying conditions could leverage the strengths of these different modeling approaches. Efforts to adapt or develop new models designed to generate biomass estimates suited for estimating carbon flux values (rather than borrowing existing models designed for other purposes) would provide a platform to use existing data and information to extrapolate carbon dynamics to regional and global scales.

Mesopelagic fishes can be approached in models from below by expanding nutrient-phytoplankton-zooplankton models to include fish-focused compartments. Anderson et al. (2019) used a simple food web model that starts with assumed primary production that is then followed through a detrital pool and five biological groups to generate biomass estimates of mesopelagic fishes. By specifying how the carbon flows through these pathways via grazing and growth relationships of the predator–prey linkages, and balancing the food web to be in steady-state, they estimated the biomass of meso-pelagic fishes to be 2.4 Gt C with large uncertainty. An

extensive sensitivity analysis showed that the estimated probability distribution of biomass was approximately log-normally shaped (thick tailed) with a mode near 1.0 and extreme high values of 10–12 Gt C. Model sensitivity analyses highlighted the importance of uncertainty in two key areas: (1) the extent and efficiency to which mesopelagic copepods are sustained by detritivory and (2) the longevity and physiology of mesopelagic fishes. This sensitivity analysis provides guidance for specific focal areas of research that could be addressed to reduce uncertainty in future biomass estimates, and therefore can provide a template for modeling approaches moving forward.

From biomass to estimation of export flux

Estimation of carbon flux below the ocean's surface will involve a combination of monitoring data, empirical information on fish physiology, feeding, and metabolism, and a variety of assumptions about the biogeochemical composition and elemental ratios of the fish and their prey. Therefore, a notable limitation for these approaches is that the data needed for predicting carbon fluxes on regional and global scales is missing for key fish groups. Candidate approaches can be found by modifying the usual methods for estimating material fluxes in the ocean. Some candidate approaches are: (1) size-spectrum and macroecology, (2) static ratio-based methods, (3) bioenergetics models, (4) primary production to biomass of fishes to downward flux, and (5) aquaculture. We list the types of approaches as distinct methods but there is overlap and sharing of components across methods. Our list should be viewed more as pieces that can be assembled in different ways and in a step-wise approach depending on the specifics of the question and the availability of the information. All of the methods use some form of biomass in their calculations as a starting point and end with estimates of carbon flux below the depth where significant upward mixing would occur. The assumption is that the carbon that passes this depth will not return to the upper water column.

Size-spectrum and macroecology

Size-spectrum models organize the biomass of organisms from phytoplankton to fishes into size intervals and use allometric relationships to compute material fluxes between size classes. This approach has a long history in modeling marine ecosystems (e.g., Platt and Denman 1977) and has been used to model species abundance (Andersen and Beyer 2006), biomass of fishes (Jennings and Collingridge 2015), and the vertical flux of organic carbon from pelagic ecosystems (Legendre and Michaud 1998). The approach has important advantages and disadvantages. For example, size-spectrum analysis relies on the assumption that physiological processes contributing to carbon flux are strongly dependent on organism body size that is easy to measure. However, size may not be sufficient in some cases, and environmental variables may also play a significant role. For example, allometric relationships for the

respiration rate of mesopelagic fishes underestimate respiratory fluxes in colder ocean waters (Belcher et al. 2020) indicating that temperature should be considered as well as body size. Such allometric relationships are developed from measurements of individuals in a laboratory and may not be directly transferrable to estimating metabolism in the field. This is in part because of the high variability seen in the allometric relationships that can reflect interindividual and local variability of physiological rates in the population (White and Kearney 2014). The simplification that scaling models provide comes at the cost of losing taxa-specific results that can potentially be important in regions where community composition shows large changes. In spite of these caveats, size spectrum models provide a tractable way to model carbon export from fishes.

Ratio-based methods

Ratio-based methods start with biomass and make a series of chain calculations of rates and ratios to obtain estimates of carbon flux. This method is related to the size-spectrum approach but is more general, allowing for traits other than size to drive the analysis and using ratios that include but are not always allometrically based. Longhurst et al. (1990) used seven size classes of plankton and nekton at specific sampling stations and computed the flux of carbon to the depth of the permanent density discontinuity. They started with primary production and used empirical relationships between primary production and particle flux to compute the downward flux, and used respiration rates, converted to carbon equivalents, to estimate carbon released from vertical migrators when they were in the surface waters. They estimated carbon fluxes to the deep of $\sim$ 20–430 mg C d^{-1}, which was $\sim$ 13% and 58% of the particulate sinking flux. When they scaled these station-based estimates to the area of the ocean with similar habitat, they reported a global respiratory flux up to 0.72 Gt C yr^{-1}. Longhurst et al. (1990) noted many uncertainties in their calculations. To our knowledge, ratio-based approaches have not been used to specifically estimate global fish-based carbon flux, presumably because data requirements may be more complex for higher trophic levels with increased mobility. However, Cavan and Hill discuss the link between primary production, fisheries production and carbon flux through fishes. Schiettekatte et al. (2020) combine C, N, and P ratios in food with minimum dietary requirements of fishes to estimate nutrient flux through fishes; however, estimates for carbon flux were not reported.

Bioenergetics models

This approach focuses on the growth of individual fish by representing the ingestion, respiration, excretion, and egestion processes. Typically, these processes are functions of body weight or size and temperature. The net energy is then used to increase body mass or to contribute to reproductive products. By modeling the detailed bioenergetics of an individual, the scaling up to the population-level to get to carbon fluxes is conceptually straightforward. There are two major approaches used to represent the bioenergetics of individuals: Wisconsin formulations and Dynamic Energy Budget. Both approaches are easily scalable to the cohort, population, and community levels either by multiplying the energetics results for an individual by the abundances and sizes of individuals from field data or by imbedding the bioenergetics models (i.e., growth of individuals) into models of population dynamics that account for the additional process of reproduction and mortality (Luo and Brandt 1993; Maury and Poggiale 2013; Sibly et al. 2013).

The Wisconsin model (developed by Kitchell et al. 1974, 1977; updated in Deslauriers et al. 2017) considers consumption, respiration, specific dynamic action, egestion, excretion, and egg production as inclusion terms. Growth is typically estimated from the model, and the approach does not incorporate mortality and reproduction. The inclusion terms are not independent, as consumption patterns affect all other parameters in the model equation. Although there are many versions of the equation, typically consumption is the only term that is changed and the waste product is assumed to be $\sim$ 0.2. There are ongoing efforts to decouple the models and incorporate food availability to reflect more realistic conditions that would ultimately impact carbon flux outputs. The Dynamic Energy Budget approach was also developed to model energy inputs, storage, energy allocation (to growth, somatic maintenance, reproduction), and waste outputs in individual fish (e.g., Jusup et al. 2011). The big difference between the Wisconsin and Dynamic Energy Budget models is that in a Dynamic Energy Budget, the energy allocated towards growth and reproduction can be adjusted according to fish species and size. Bioenergetics approaches are also applied to Eulerian models (i.e., Atlantis and EwE) to simulate the changes in biomass, rather than individuals. Bioenergetics models can be data hungry, and therefore increasingly uncertain when applied to taxa such as mesopelagic fishes where physiological data are lacking, and there are few closely comparable species.

Primary production to biomass of fishes to downward flux

As we can derive biomass of fishes from carbon fluxes using primary production and trophic efficiency through the food web, we can also use primary production to derive downward fluxes of carbon in the ocean. This approach can be considered a subset of the ratio-based approach; we emphasize it here because it includes not only using primary production to estimate carbon fluxes but also to estimate biomass of fishes, which is a major uncertainty. These methods use either observed temperature and chlorophyll distributions (e.g., Behrenfeld and Falkowski 1997) or mass, energy, and fluid motion constraints from light and nutrient limitation through coupled circulation-biogeochemistry models to estimate primary production and then apply transfer efficiency functions to calculate biomasses and their contributions to downward carbon fluxes. The strength of both approaches

(ratio and primary production) is the strong relationship observed between chlorophyll and fishes (Maury et al. 2007; Christensen et al. 2009; Friedland et al. 2012; Stock et al. 2017).

Aquaculture

Aquaculture models have been developed to estimate the flux of particulate material to the bottom from in situ facilities, such as cages and pens. The goal of these models was to determine how the unused food and fish-produced fecal waste products, from a constrained location with highly concentrated fish, would impact the benthic environment underneath the facility and downstream. There are parallels between computing material flux to the bottom from aquaculture facilities and computing contribution of fishes to carbon flux to the deep ocean. Aquaculture impact assessment can provide foundational information for the ratio-based and bioenergetics approaches for estimating carbon flux in the ocean. Several models have been proposed for the impact assessment of aquaculture (Hall et al. 1990; Cromey et al. 2002; Corner et al. 2006; Rensel et al. 2006; Chamberlain and Stucchi 2007; Campuzano et al. 2015; Brigolin et al. 2016). The models are similar to the bioenergetics models except that the biomass (fish weight), growth rate, and food availability terms are known and the model incorporates a benthic component to estimate the flux of carbon, nutrients, and material to the bottom. For example, DEPOMOD (Cromey et al. 2002) models the deposition and biological effects of solid wastes (unused food and feces) by tracking this waste as particles to see the fate of the waste (i.e., advection, settling, resuspension), and then incorporates a benthic component. The AQUA model (Rensel et al. 2006) similarly incorporates unused food waste and fecal material, and once this particulate waste reaches the bottom, the benthic community response is modeled. These models provide information on formulation of processes, parameter values, and ratios for adaptation to ocean and continental shelf calculations of carbon flux, but again their application to estimates of global carbon flux is limited by a lack of detailed physiological data, especially on mesopelagic fishes, and scaling issues to go from simplified spatial structure of project level analysis (i.e., aquaculture facility) to regional estimates.

Passive flux

Increasing our confidence in estimating passive flux requires a combination of laboratory and field approaches. Laboratory experiments can provide fecal pellet organic and inorganic carbon content, and their production and sinking rates, to expand the limited measurements presently available. A synthesis of these values can then be applied to fish abundance or biomass values in situ. These efforts should initially be focused on epipelagic species that could be maintained in a laboratory setting. Another priority (albeit challenging) is for additional field measurements that target mesopelagic fishes.

A possible strategy would be to expand (by species, geographically, temporally, and adding sinking rates) on the work initiated by Hidaka et al. (2001), whereby gut contents of mesopelagic fishes would be collected and measured for carbon content and sinking rate. This, however, still requires metabolic assumptions to be made on the rate of fecal pellet production. A focus here could be on biomass-specific (not species-specific) fecal pellet production and sinking rates generalized from a sufficiently diverse set of species. Repeated laboratory experiments (epipelagic) and field experiments with gut contents (especially for mesopelagic fishes) using multiple species of different sizes could provide fecal flux: biomass and allometric relationships that could be applied more broadly.

Another approach to better estimate fecal production rates for passive flux is through enumeration of the relationships of fecal production to daily intake and respiration (e.g., Hidaka et al. 2001; Davison et al. 2013; Hudson et al. 2014). However, these rates are dependent on many factors (e.g., temperature, diet, season). Experiments, field data, and models would need to carefully consider how to incorporate the influences of these factors to ensure that general and robust relationships are developed. An example of this is the approach taken by Schiettekatte et al. (2020), whereby limiting nutrients are used as the minimum parameter for consumption and excretion rates, and factors such trophic level, life stage, and temperature are considered where possible, using well-established open-access databases. Experimental design and laboratory/field data collection should consider that the results will be applied as model inputs, used for other species, and extrapolated spatially to estimate regional and global fish carbon flux. Therefore, these approaches should also incorporate field-relevant maxima and minima values of production and sinking rates so that variability can be propagated when results are used for extrapolation. Uncertainty analysis of the extrapolation schemes can then identify which parameters contribute most to uncertainty and highlight target areas for additional research.

Recent developments in optical sensors designed to detect backscatter-derived POC are promising because they can detect smaller particles and they have been integrated into multiple autonomous platforms (Bio-Argo floats: Dall'Olmo and Mork 2014; Gliders: Alkire et al. 2014; Bol et al. 2018). Autonomous platforms can provide high temporal and spatial (horizontal and vertical) resolution that can address observational gaps, questions posed about drivers that control carbon flux variability, and the dynamics of remineralization processes. These sensors measure volume scattering function at different wavelengths. The measured values of volume scattering function is obtained for particles by adjusting for seawater and POC is then estimated from particle backscatter using depth-dependent conversion factors derived using in situ POC measurements (described in Alkire et al. 2014; Bol et al. 2018). These sensors are limited, however, in that they cannot differentiate among types of

particles. Therefore, to estimate fish-based fecal carbon flux using this approach, additional conversions are required, specifically the proportion of POC derived from fishes, which itself can be highly variable in time and space. Use of other in situ imaging, such as the Underwater Video Profiler (UVP) that distinguishes between particle types and provides particle measurements, would also be beneficial.

Further consideration of how to estimate the inorganic carbon flux should focus on the mineralogy and solubility of the carbonate minerals produced by mesopelagic (and then other) fishes and how they determine the amount excreted and the rate of dissolution during sinking. In the case of animals like myctophids, which are notorious for faring poorly during prolonged periods in captivity, this may mean conducting short-term experiments aboard research vessels or using representative surrogate species that can survive in laboratory settings and share similar physiology in terms of carbon fluxes. If future studies determine that the carbonate mineralogy and morphology of a few common mesopelagic fish species (or surrogate species) is consistent with that of shallow tropical, subtropical, and temperature fishes, then these data can be combined and confidently scaled up to the community and applied across regions. Additional data (laboratory and/or field) will improve the estimation of inorganic carbon fluxes to depth by enabling further understanding and quantification of: (1) the influence of fish on the enhancement of seawater alkalinity with depth and (2) the feedback effect of this dissolution (and hence loss of denser carbonate) on the slowed sinking rates of the POC component of fecal pellets. This complex set of potential interactions has only been addressed with limited data and as separate components. Also important for accurate extrapolation will be information on precisely where (i.e., at what depths) fecal pellets are released by the mesopelagic fishes. For those undergoing diel vertical migrations, most of the carbonate-rich fecal pellets could conceivably be egested near the surface. This would not only maximize the quantity of inorganic carbonate dissolution near the surface (the "upward alkalinity pump", Roberts et al. 2017), but could also maximize the chance of organic carbon decomposition during sinking. If the data show the majority of fecal pellets are released deeper, then there would be little opportunity for an upward alkalinity pump and only limited decomposition would occur before the carbon enters the deeper ocean.

Active flux

Overcoming challenges in measuring the active carbon flux of fish depend on obtaining not only better biomass estimates of DVM fishes, but also more extensive measurements of physiological rates that can be confidently applied to various fish taxa. As discussed above, time-averaged field metabolic rates are more relevant to discussions of carbon flux than standard or routine metabolic rate. Measuring metabolic rates of mesopelagic fish taxa directly using in situ respirometry is

presently underway (B.H. Robison pers. comm.) and requires specialized sampling capabilities such as remotely operated vehicles or other submersibles. Allometry and electron transfer system measurements should provide confident values of sustained (field) metabolic rate, requiring taxon-specific transfer equations to convert enzyme activity data to, for instance, oxygen consumption rates (Ikeda 2016; Belcher et al. 2020).

Newly emerging proxies aimed at estimating field metabolic rates from the proportion of respiratory carbon in otolith biominerals (Chung et al. 2019*a,b*) offer considerable promise. The otolith-based proxy is relatively cheap and can be applied retrospectively potentially allowing large data sets of individual metabolic rate information to be obtained from archived otoliths or newly collected samples. The otolith approach has been applied successfully to determine differences in relative field metabolic rate among myctophid fishes from the Southern Ocean (S. Alewijnse unpubl.). However, much like the electron transfer system approach, the otolith method for estimating metabolic rate also requires a conversion from the proportion of respiratory carbon in otoliths to a comparable metric such as oxygen consumption rate.

Finally, fluxes from fishes are not all created equal. Vertical carbon flux from epipelagic fishes in both coastal and open ocean environments may be dominated by passive fecal flux, whereas respiratory flux is likely the highest contributor of carbon flux in DVM mesopelagic fishes. Because these relative contributions may vary, future attempts to estimate global fish-based carbon fluxes will need to apply knowledge of the processes controlling fish-based carbon flux to three broadly defined ocean biomes (regions characterized as oligotrophic, upwelling, and seasonally stratified coastal) and constrain these estimates based on proportions of epipelagic and mesopelagic fishes. Conversely, one could utilize observations and apply models to determine spatially explicit fish-based fluxes for the three ocean biomes and then calculate a global flux based on specific habitat area or volume. In addition, consideration of the community composition (and life cycles and life histories) of the species present in different regions and seasonally will allow important further refinement of the estimation of regional and global active fluxes of carbon by fishes.

Actionable recommendations

The research conducted thus far has been invaluable in recognizing the potentially significant role fishes play in carbon flux and the biological pump, and the data and modeling have also highlighted significant challenges and knowledge gaps that limit our ability to quantify fish contributions to total regional and global carbon fluxes. Given the ongoing impacts that harvest and climate change pose to fish stocks, and how these changes (including associated food web and biogeochemical responses) would translate into spatial and temporal variability in contributions of fishes to carbon dynamics, an investment in further research to quantify

biomass of fishes and associated carbon fluxes is timely. The mesopelagic zone, because of the high biomass of fishes, their potential to generate downward carbon fluxes, the increasing attention to these species as a possible harvestable resource (Hidalgo and Browman 2019; Martin et al. 2020), and potential impacts of deep-sea mining waste plumes in this habitat (Drazen et al. 2020), is an especially high priority. Furthermore, because fishes provide other benefits to humans (nutrition, biodiversity, cultural, recreational, commercial), management decisions are currently made without understanding the trade-offs and interdependencies between these uses, their impacts and fish-based carbon flux (Martin et al. 2016; Legge et al. 2020). A recent global analysis concluded that overexploitation of fish stocks could reduce the contribution of marine fishes, particularly in carcass deadfall, to blue carbon sequestration over time (Mariani et al. 2020). The economic value of carbon storage reduced by fisheries in the eastern tropical Pacific was estimated as \$12.9 billion yr^{-1} (Martin et al. 2016), while the cost of predicted declines in the biological carbon pump in the North Atlantic by 2100 due to increasing carbon emissions was estimated at between \$170 and \$3000 billion in mitigation costs, and \$23 and \$401 billion in adaptation costs (Barange et al. 2017). Below, we list some specific actionable laboratory, field, and modeling studies, as well as key developments, that would improve estimation of the contribution of fishes to carbon cycling and enable more realistic representation of fish effects on carbon in extrapolation calculations and regional and earth system models that provide the foundation for projecting the magnitude and efficiency of existing and future carbon sinks.

Key laboratory studies

- Identify fish species for experiments that can represent functional groups of fish taxa that are quantitatively relevant to global biomass of fishes and/or global carbon fluxes. These should include species in coastal and shelf areas (e.g., small pelagic forage fishes) that are likely dominant contributors to carbon flux and amenable to field and laboratory study. Experiments on open-ocean mesopelagic species (e.g., DVM myctophids) will be more challenging. However, these challenges could be overcome if surrogate species can be identified.

- Directly determine excretion of respiratory CO_2 and DOC, fecal pellet production (both POC and PIC), and fecal pellet morphology, composition, sinking, and dissolution rates of both POC and PIC for globally dominant species or functional groups (or suitable surrogate species) to determine relative importance of these different carbon sources on overall carbon fluxes.

- Determine via new measurement, synthesis of existing information, and novel data-analysis methods robust relationships of rates and ratios for identified dominant contributors (e.g., ingestion: fecal flux, size and biomass: flux), the timing of digestion (to estimate likelihood of feces

being released in feeding or resting habitats), and the influence of temperature, habitat, and food availability on these derived relationships.

- Compare the magnitude of relative carbon fluxes among competing and overlapping fish species to make predictions on how species shifts within the fish community might impact carbon flux estimation.

- Experimentally evaluate the effects of environmental stressors (e.g., warming, deoxygenation, ocean acidification) on the rates, magnitude, and comparative source contributions of carbon released by fishes.

Key field studies

- Develop new or improved methodological approaches for in situ biomass determination of fishes (e.g., acoustics), abundance and flux estimations of fish-produced fecal pellets using imaging systems (e.g., UVP system), and estimation of fish-based passive flux using sediment-based measurements (e.g., lipids, stable isotopes, eDNA).

- Compare the performance (precision and accuracy) of different methodological approaches (net tows, sediment traps, electron transfer system, ship or glider acoustics, optical POC measurements) for estimating biomass of fishes with the endpoint of using the biomass estimates to estimate carbon flux.

- Measure respiration rates using the electron transfer system and otolith isotope approaches to improve calibration between respiration or oxygen consumption rates, electron transfer system activity and the proportion of respiratory carbon in otolith biominerals. Then apply these measurements across ranges of mesopelagic functional groups, body sizes, temperatures and seasons to refine assumptions of allometric scaling of respiratory variables.

- Expand field efforts to multiple regions and ecosystems (including across biogeographic ecoregions within the mesopelagic) and that include simultaneous measurements on fish- and zooplankton-mediated carbon export, as well as total export, in order to improve and refine regional and global model estimates and the uncertainties of fish-based carbon flux relative to other sources of carbon fluxes.

- Incorporate time-series observations and measurements in key locations (e.g., productive coastal ecosystems, open ocean regions with high myctophid biomass) to determine diurnal, seasonal, and interannual dynamics of fish-based carbon flux in different representative ecosystems.

- Leverage existing facilities for research, including coastal aquaculture pens and aquariums that offer different degrees of realism between the laboratory and true field conditions.

Key model developments and improvement

- Comparative analysis, synthesis, and potential unification of existing models that, with little or moderate modification, can be used to generate carbon fluxes from fishes. Presently, candidate approaches and existing models are

spread over multiple focus areas (e.g., fisheries stock assessment, size-spectrum, bioenergetics, regional-scale, biogeochemistry, nutrient-phytoplankton-zooplankton, food web, impacts of aquaculture) that operate with limited cross-fertilization. A unification of these approaches and models for quantitative representation of fishes in the carbon cycle, perhaps first with example case studies, would provide critical context for new understanding.

- Merge laboratory results with existing field data and new field data from emerging technologies to derive robust rate relationships for biomass: rate ratios and flux dependency on temperature, region, food availability, and other drivers that have documented and quantified biases and uncertainties.

- Augment individual-based bioenergetics and Dynamic Energy Budget models to simulate details of respired, excreted, and egested carbon for a few well-studied fish species in order to examine mechanistic aspects of fecal pellet production rate, ingestion : fecal flux, sinking, PIC : POC ratio, composition and geometry of excreted material, and commonly used conversion factors.

- Conduct model sensitivity analyses which, in detecting sources of uncertainty in models and model inputs, would identify the critical information needs to quantify fish-based carbon flux.

- Compute carbon export potential of different functional groups with the data presently available on well-studied species to provide additional estimates of fish contributions and also to work backwards from modeling carbon fluxes in order to provide a strategic roadmap for the design of laboratory and field data collection.

- Adapt existing data assimilation methods that can test models using diverse sources of data with limited knowledge of the higher-order properties (e.g., covariance, probability distributions) of the data including application of machine learning and artificial intelligence methods.

- Link laboratory studies (mentioned above) with models to enable projection of potential changes in carbon flux, including contributions of fishes, under ongoing climate change.

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Conflict of interest

None declared.