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Mesopelagic fish biomass in the southern California current ecosystem

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ABSTRACT

Mesopelagic fishes are the most common vertebrates on Earth, forming an important link between lower trophic levels and higher predators, and also between surface production and the deep sea. The biomass of these fishes is a key parameter for ecological modeling of oceanic ecosystems, but it is poorly known. The two most common methods to estimate the biomass of these fishes, acoustic and trawl surveys, are both sensitive to the ability of fishes to avoid nets. We show that size-dependent changes in trawl capture efficiency can affect acoustic estimates of biomass estimates 5-fold. We used both acoustic and trawl-based methods (informed by morphological data and acoustic modeling of individual backscattering) to estimate the biomass of mesopelagic fishes of southern California to be 25–37 g m^{-2} of ocean surface, a comparable density to that of inshore epipelagic zooplanktivorous fishes. Our results indicate that mesopelagic fishes are likely to play a major role in regional food webs.

1. Introduction

The "Lilliputian fauna" (Murray and Hjort, 1912) that inhabits the mesopelagic zone between approximately 200 and 1000 m depth has fascinated scientists since it was discovered more than a century ago. Much has since been learned about this unique fauna and its morphological, physiological, and ecological adaptations to the limited light and food available in this zone, but the role that this fauna plays in global marine food webs and biogeochemical cycling still remains poorly understood. Mesopelagic fishes, the dominant component of this fauna, are found throughout the open ocean, and a significant proportion conduct diel vertical migrations (DVM) to feed on near-surface zooplankton under cover of darkness. They are thus a key link between the plankton and higher predators in marine food webs, as well as a potentially significant conduit for the active transport of organic matter from the surface to the deep ocean. However, mesopelagic fishes are often neglected in models of marine food webs and carbon cycling or considered to be relatively minor players, largely due to uncertainty with regard to their biomass.

In the only global review of mesopelagic fish abundance to date, Gjosaeter and Kawaguchi (1980) estimated their global biomass to be on the order of one billion tonnes, based primarily on trawl surveys. Gjosaeter and Kawaguchi (1980) recognized that their estimate might be significantly biased due to avoidance of small trawls and escapement through the meshes of large trawls, but believed it to be within a factor of three of these fishes' true abundance. However, more recent studies indicate that the biases due to avoidance and escapement from pelagic trawls may be even more severe, such that there may be an order of magnitude or more midwater fishes than previously recognized (Kaartvedt et al., 2012; Koslow et al., 1997; May and Blaber, 1989).

More recent estimates of mesopelagic fish abundance that have relied on acoustic as well as trawl sampling have generally supported the view that trawl sampling grossly underestimates midwater fish biomass (Davison, 2011b; Kloser et al., 2009; Koslow et al., 1997). However, acoustic sampling of midwater assemblages contains its own uncertainties and potential sources of bias.

First, combined acoustic/trawl surveys depend on the trawl sampling to assess community composition. Key components of midwater assemblages that may comprise a significant proportion of the acoustic backscatter may be missed entirely by midwater trawling, such as thecosomatous (shelled) pteropods, fragile siphonophores with gas-filled pneumatophores, large fishes, and squids. Over the continental slope, the relative mix of mesopelagic and benthopelagic fishes near the bottom is often uncertain, while at night, some mesopelagic fishes may migrate into the upper 10 m of the water column and be unobserved by hull-mounted acoustic systems (O'Driscoll et al., 2009).

Several further issues complicate the modeling and assessment of the acoustic backscattering from mesopelagic fishes. Small mesopelagic fishes may exhibit resonance at the frequencies generally used for acoustic surveys (e.g., 18 and 38 kHz). The gas-filled swimbladders of some taxa regress and become fat-invested through ontogeny (Butler and Pearcy, 1972; Davison, 2011a; Yasuma et al., 2010), so their target strength may decline markedly with size. If present, a gas-filled swimbladder accounts for 90% or more of a fish's acoustic backscattering (Davison, 2011a;

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Foote, 1980). As a result, the simple positive relationship of target strength (TS) with length observed in many coastal fishes (e.g., Foote and Traynor, 1988) will not be obtained. Swimbladder inflation in relation to depth will also presumably greatly influence TS, but this is also uncertain for midwater fishes: to what extent do they inflate their swimbladders at depth, given the energetic costs of extracting oxygen from the often oxygen-poor water at depth and the need to resorb the gas as they vertically migrate into near-surface waters?

Uncertainty of an order of magnitude in the abundance of a potentially key group of zooplankton consumers has considerable implications for our understanding of pelagic ecosystem structure and function. The dynamics of productive eastern boundary current ecosystems are often considered to be regulated by a few key species of epipelagic planktivores, such as sardine and anchovy, which are believed to dominate this trophic level. Based on this "wasp-waist" paradigm, fluctuations in the abundance of these few key taxa are critical to the dynamics of a wide array of their zooplankton prey and their higher predators, while the potential role of mesopelagic zooplanktivores is generally ignored (Cury et al., 2000). Similarly, carbon export models have generally ignored the role of mesopelagic fishes in active transport of carbon from near-surface waters to the deep ocean (Buesseler et al., 2007; Falkowski et al., 2003; Longhurst et al., 1990). However, if estimates for the biomass of the mesopelagic micronekton are revised upward by an order of magnitude, their role in marine food webs and the ocean carbon cycle may need to be re-evaluated (Davison et al., 2013).

In this paper, we assess the biomass of mesopelagic fishes using acoustic and pelagic trawl sampling on cruises of the California Cooperative Oceanic Fisheries Investigations (CalCOFI) off southern California (Fig. 1) over three years (2010–2012). We are not able to resolve definitively the full array of potential biases and uncertainties in such sampling. However, we attempt to confront them in order to examine the sensitivity of biomass assessments to them. We view this as a necessary step to focusing research so that the most critical sources of error and uncertainty can be resolved.

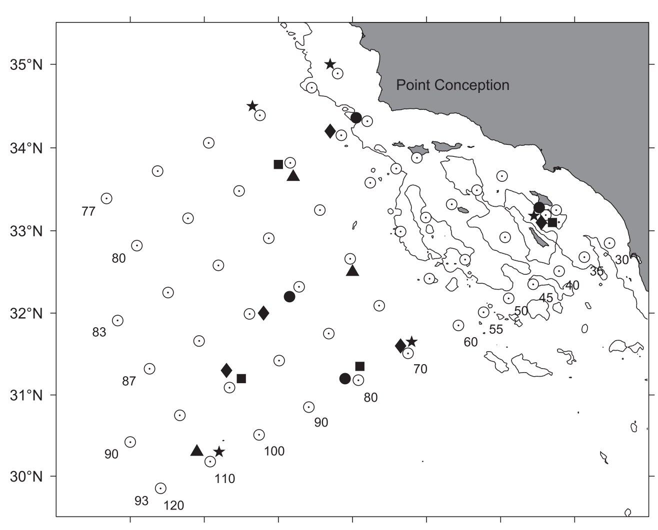

Fig. 1. CalCOFI stations (open circles with dots). Isobaths are shown for 1000 and 2000 m. Line numbers are shown at the offshore terminus, and station numbers are shown to the south of Line 93. CalCOFI stations are referred to in "line.station" format (e.g., 93.70). Approximate trawl locations are shown as closed circles for CalCOFI-1008; closed triangles for CalCOFI-1011; closed squares for CalCOFI-1108; closed diamonds for CalCOFI-1110; and closed stars for CalCOFI-1202.

2. Methods

2.1. Data collection

Midwater trawl samples and acoustic backscattering data were collected from seven CalCOFI cruises between 2010 and 2012 (Table 1) to estimate mesopelagic fish biomass in the southern California Current Ecosystem (CCE). Samples were collected along the CalCOFI grid from San Diego to north of Point Conception (Fig. 1).

Oblique tows were made to ~500 m depth using a 5-m^2 Matsuda–Oozeki–Hu trawl (MOHT) fitted with a 1.7 mm uniform-mesh net (Oozeki et al., 2004). In deploying the net, the ship speed was maintained at 4 knots while 1500 m of wire was released at a speed of ~40 m min^{-1}. Net retrieval was carried out at a ship speed of ~3 knots with the wire recovered at ~25 m min^{-1}. A total of 22 tows (21 in daylight, one at night) were made at various CalCOFI stations with the aim of collecting samples from inshore basins and continental slope, the core of the California Current, the productive upwelling region near Point Conception, and oligotrophic offshore waters. Three to five tows were made per cruise for five of the seven cruises (Fig. 1). Trawl depth was recorded using a Wildlife Computers Mk9 archival tag fixed to the frame of the MOHT. Water flow through the net was measured with a TSK flowmeter. Samples were preserved in 5% formalin within one hour after recovery of the net. Ashore, fishes were identified to species and standard length (L_s) measured to the nearest millimeter. Wet weight of fishes was either directly measured to 0.01 g precision, or calculated from length–weight curves (Table 2). Abundance and biomass were estimated by dividing the number and weight (respectively) of captured fishes by the volume of water filtered, and then multiplying by the depth of the trawl.

Acoustic backscattering data were collected between stations using a hull-mounted Simrad EK60 split-beam echosounder equipped with five frequencies (18, 38, 70, 120, and 200 kHz). The EK60 was calibrated before each cruise using the standard sphere method (Foote et al., 1987). Pulse length was set to 1.024 ms with a ping rate of 0.5 s^{-1}. Beam angles were 7° for the 38 kHz transducers and 11° for the 18 kHz. Power for both 18 and 38 kHz transducers was 2 kW. As the three highest frequencies did not reliably penetrate to the depth of the daytime deep scattering layer (DSL) at the vessel transit speed (~10 knot), they were not used in this study. Acoustic data were processed and noise removed using Echoview software. Nautical area scattering coefficient (NASC) was calculated over 100 m distance segments by 5 m depth intervals. Only backscattering data from 175 to 525 m were used for analyses, corresponding to the shallowest daylight occurrence of mesopelagic fishes and the depth of the trawls. Although some mesopelagic fishes are found in the epipelagic at night, they are mixed with abundant epipelagic fauna that are poorly sampled by our net, and thus we excluded data shallower than 175 m.

Table 1
CalCOFI cruises for which data were collected.

Cruise nos.	1001	1008	1011	1101	1108	1110	1202
Month	January	August	November	January	August	October	February
Year	2010	2010	2010	2011	2011	2011	2012
No. of trawls	0	4	3	0	5	5	5
Acoustic data?	Yes	Yes	Yes	Yes	Yes	Yes	Yes