



## Near-island enhancement in mesopelagic micronekton assemblages off Hawai'i

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### ABSTRACT

The west coast of Hawai'i Island hosts elevated primary production compared to offshore waters and an abundance of large pelagic animals for reasons that are not entirely understood. Here we show that the nearshore environment off the west coast of Hawai'i exhibits an increased biomass and abundance of mesopelagic micronekton. Acoustic surveys from this study and prior work show a higher nautical area scattering coefficient (as a proxy for biomass) in a deep non-migratory layer in nearshore sites compared to offshore sites that is persistent over five years. Cobb trawl samples taken at the depths of the deep scattering layer (~450 to ~550 m) in 2016 and 2017 showed 1.3 to 2.2 times higher biomass and 2.7 times higher abundance nearshore (~4 km from shore) compared to offshore (~24 km from shore). Fishes dominated the trawl catches and a large fraction of the nearshore enhancements were due to Sternoptychidae and Serrivomeridae across both years. In contrast, Melamphaeidae consistently were more abundant and had greater biomass offshore. This deep scattering assemblage contrasts with the mesopelagic boundary layer assemblage by being nonmigratory and taxonomically different in composition. These nearshore mesopelagic enhancements could occur as the result of increased nearshore food supplies deriving from Island Mass Effect enhanced primary production or from advection and concentration in a complex flow environment in the lee of the island. Regardless of mechanism, this temporally persistent, high biomass, largely nonmigratory layer of mesopelagic micronekton is different from the better known migratory mesopelagic boundary layer assemblage and may provide food to deeper diving marine mammals and pelagic fishes possibly explaining the aggregation of large pelagic animals in this region.

### 1. Introduction

Mesopelagic micronekton, small fishes, crustaceans, and cephalopods ~2 – 20 cm in length, are key players ecologically and biogeochemically in the ocean. Much of the mesopelagic micronekton undertake diel vertical migrations (Klevjer et al., 2016), inhabiting deeper waters during the day to seek refuge from predators, then rising through the water column at night to feed on plankton (Hays, 2003). This diel movement represents the largest daily migration of animals on Earth (Hays, 2003; van Haren and Compton, 2013). As such, micronekton play a key role in nutrient transfer between the ocean's vertical

divisions, leading to carbon sequestration and climate regulation (Ariza et al., 2015; Davison et al., 2013; Saba et al., 2021). Micronekton are also prey for higher trophic level marine organisms, some of which support commercially valuable fisheries, including tuna (Brodeur and Yamamura, 2005; Catul et al., 2011). Additionally, they are targets of fisheries directly for fishmeal, and nutraceuticals such as Omega-3 fatty acids (Pauly et al., 2021; St. John et al., 2016). Quantifying what drives the abundance and diversity of mesopelagic micronekton is therefore crucial if we are to successfully predict their dynamics and impacts on ecological, chemical, and socioeconomic feedbacks within the broader ocean-atmospheric system.

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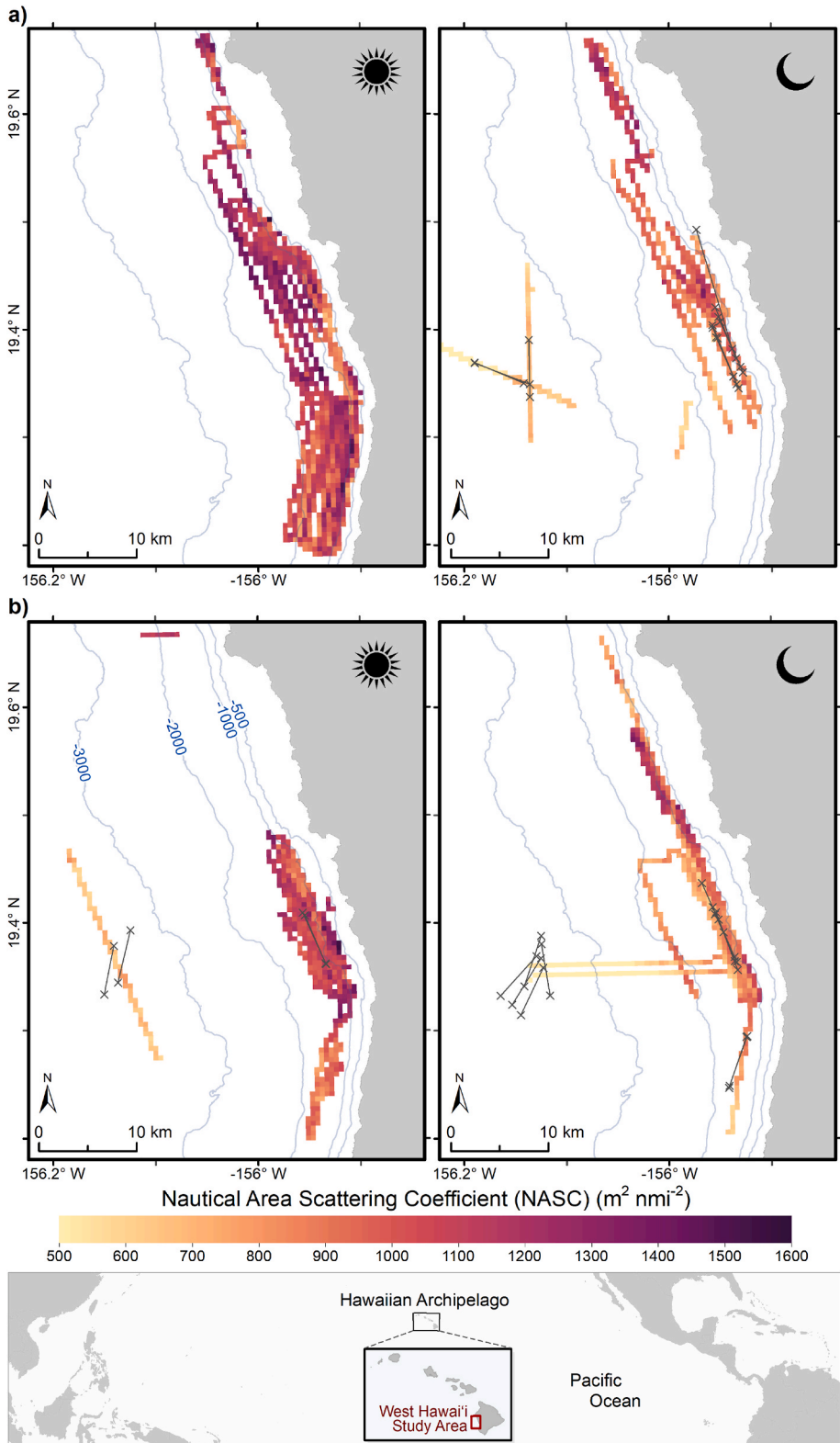
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Islands and seamounts are common features across the ocean that can alter primary production and fisheries yield for pelagic species. Nearshore environments around islands and atolls contain substantially higher phytoplankton biomass than offshore oceanic waters (Gove et al., 2016). Termed the Island Mass Effect (Doty and Oguri, 1956), this phenomenon occurs because of several interacting biogeophysical processes that boost near-island nutrient concentrations and phytoplankton

production over the full euphotic zone (Gove et al., 2016). Additionally, increased upwelling and mixing at abrupt topography such as shallow seamounts, can also enhance primary production, which can result in an increased biomass of zooplankton if residence times of upwelled water and retention of plankton are sufficient (Genin, 2004; Leitner et al., 2020). Some islands and seamounts exhibit higher pelagic fish catch (e. g. tuna) than the neighboring open ocean (Morato et al., 2010), in some



**Fig. 1.** 70 kHz day time and night time acoustics transects in a) September 2016 (pulse length of 1024  $\mu s$ ) and b) April 2017 (pulse length of 512  $\mu s$ ) showing mean deep-scattering layer nautical area scattering coefficient (NASC;  $m^2 nmi^{-2}$ ) at 400 – 600 m depth along West Hawai'i (cell size of  $500 \times 500$  m in UTM 5N projection). Cutaway shows the location of West Hawai'i in the Pacific Ocean. 'X' marks start and end of trawls, with the line representing the trawl distance at each location. Depth contour lines (or isobaths) are shown in blue and labeled with depth in meters in the bottom left panel.

cases driven by bottom up forcing (Leitner et al., 2020). However, the extent to which the Island Mass Effect or seamount-stimulated primary production influences mesopelagic micronekton and higher trophic levels around tropical islands and extending into deeper waters beyond the euphotic zone is not well understood.

Shallow topography or abrupt changes in topography can alter micronekton without increases in primary production. They may disrupt or truncate the normal downward migrations of mesopelagic organisms, resulting in concentrations at dawn near shallow seafloors surrounded or flanked by deep water (Cascão et al., 2017; Porteiro and Sutton, 2007; Rogers, 2018). Apparent avoidance of such topographies has also been noted (Christiansen et al., 2009; De Forest and Drazen, 2009). In Hawai'i, a distinct community of mesopelagic organisms occur, called a mesopelagic boundary layer assemblage. This assemblage includes some species unique to the island flanks and is comprised of numerous fishes, shrimps, and squids, many of which undergo diel vertical migrations (Reid et al., 1991; Wilson and Boehlert, 2004). Furthermore, organisms of the mesopelagic boundary assemblage undergo a diel horizontal migration towards the nearshore in addition to their vertical migration, entailing up to an 11 km roundtrip each night (Benoit-Bird et al., 2001).

The west coast of Hawai'i Island is very ecologically rich. There is a nearshore increase in phytoplankton biomass of up to 30% higher than offshore oceanic waters in the region (Gove et al., 2016). This coast supports a high abundance and diversity of marine mammals and large pelagic fishes, including tuna and swordfish (Abecassis et al., 2015; Seki et al., 2002). Many of these organisms directly consume mesopelagic micronekton (Bertrand et al., 2002; Brodeur and Yamamura, 2005; Choy et al., 2016) and previous analysis of shallow nighttime trawl data found nearshore tows to be abundant in the mesopelagic boundary layer fauna. Interestingly, in addition to the shallow fauna, acoustic data in the region found a nearshore enhancement of deep *non-migratory* micronekton at 400 – 600 m depth (Abecassis et al., 2015). While nearshore migratory faunas of islands and seamounts have been documented before, a non-migratory assemblage of high abundance or biomass had not been previously described. This assemblage has never been sampled directly so its composition remains unknown and its temporal persistence remains unclear. Such knowledge would enable a better understanding of why this nearshore enhancement exists and how it is trophically connected to the island ecosystem and to the large predators in the region. Here, we use acoustic and net sampling along the west coast of Hawai'i to evaluate whether the deep non-migratory enhancements persist and if there are differences in micronekton abundance and community composition between the nearshore and offshore environments.

## 2. Materials and methods

### 2.1. Deep scattering layer micronekton assemblage surveys

We conducted surveys along the west coast of Hawai'i Island (Fig. 1) aboard NOAA Ship *Oscar Elton Sette* as part of two Integrated Ecosystem Assessment (IEA) research cruises during Sep 7 – 24, 2016 (SE1606) and Apr 17 – 30, 2017 (SE1704). Hawai'i Island is the geologically newest and southeasternmost island of the Hawaiian Island chain. The west coast, henceforth referred to as West Hawai'i, runs roughly north-south and has very steep bathymetry. The high (>4000m) mountains of Hawai'i block the prevailing northeast trade winds for several miles offshore. However, the trade winds are funneled through the mountains of Hawai'i and Maui, creating a zone of mesoscale eddy formation in the ocean. Additionally, westward flowing currents are found north and south of the coastline (Lumpkin, 1998; Qiu et al., 1997).

Acoustic echosounders are commonly used to evaluate mesopelagic animal distributions and biomass. The swim bladders of fishes reflect and scatter sound in the water column and can be measured by the acoustic backscatter (Perelman et al., 2021; Proud et al., 2017), which is then converted to a Nautical Area Scattering Coefficient (NASC,  $m^2 nmi^{-2}$ ). The NASC is often used as a proxy for biomass assuming that the

species composition, and as a result the scattering properties, do not change significantly (MacLennan and Simmonds, 1992). We use this proxy here noting that changes in assemblage composition can affect this metric along with changes in biomass (e.g. Dornan et al., 2019). Here, active acoustics were run continuously for the full length of both research cruises (day and night) to quantify the distribution and biomass of micronekton. A calibrated (Demer et al., 2015; Foote et al., 1987) Simrad EK60 echosounder was used to measure acoustic backscatter, with a pulse length of 1024  $\mu s$  in 2016 (consistent with data collected in the same region in 2011 (Abecassis et al., 2015)), and 512  $\mu s$  in 2017 for increased resolution (consistent with data collected in the same region in 2013 and 2014 (Abecassis et al., 2015)). To sample the acoustic backscatter, we recorded data from the 38 and 70 kHz frequencies in both survey years. For both cruises, the power was set to 2000 W and 750 W for the 38 and 70 kHz, respectively. The 38 kHz data are useful for sampling the whole deep scattering layer (>1000 m depth), whereas, the 70 kHz enables the sampling of sometimes smaller organisms and certainly those with different acoustic properties (to ~670 m depth). Previous examination of NASC depth profiles in the study region identified peaks in backscatter at 38 kHz at 400 m depth during the day time and close to the surface at night, and a persistent peak at 70 kHz between 400 and 600 m depth in the deep scattering layer (Abecassis et al., 2015). This deep scattering layer was present during both the day and night time, suggesting that as well as the migratory micronekton, there was also an abundant non-migratory micronekton assemblage present in the nearshore environment (Abecassis et al., 2015). We therefore focused on the analysis of the 70 kHz data from 400 to 600m in this study to estimate micronekton abundance in the deep scattering layer. The data was continuous but we used the 2000m isobath as the dividing line between nearshore and offshore for statistical comparisons.

Acoustic data do not provide taxonomically resolved information, so we paired our acoustics surveys with midwater dual-warp Cobb trawls to quantify the biomass, abundance and assemblage composition of the micronekton during the day time (offshore  $n = 2$ , nearshore  $n = 2$ , 2017 only) and night time (offshore  $n = 3$ , nearshore  $n = 8$  in 2016, offshore  $n = 5$ , nearshore  $n = 7$  in 2017). Tow depths were informed using real-time analysis of acoustic data to target the deep scattering layer depths of 450 – 550 m 'Offshore' sites were on average 24.2 km from the nearest shoreline along the 3000 m isobath, while 'nearshore' sites were on average 4.1 km from the nearest shoreline along the 1000 m isobath (Fig. 1). Due to the relatively low day time replication, we use these data to visually assess for similar overall trends in biomass and abundance between day and night time trawls and all formal statistical analyses (section 2.3) were limited to the night time data only (the day time data are presented as Supp. Fig. 3).

The Cobb trawl net had an open mouth area of ~140  $m^2$ , with graded mesh to funnel organisms into the cod end, from a 152 mm mesh size at the mouth to the back segment lined with 3.2 mm knotless nylon delta mesh netting. The cod end consisted of a plankton net (1 m diameter, 5 m long, mesh size 1 mm) with a 30 cm diameter by 61 cm length plasticized canvas cod-end attached to the end of the primary net in order to prevent damage to the catch and facilitate the easy removal and extraction of captured organisms, *sensu* (Drazen et al., 2011). The same equipment was used for both the 2016 and 2017 cruises, but the inner 3.2 mm liner of the net was damaged on the first trawl in 2016 and therefore absent for subsequent trawls on that cruise. We assume that the absence of this inner lining reduced the catch of smaller organisms and therefore do not formally compare the 2016 and 2017 data. Instead, we use both survey years to look for similar spatial trends in the biomass, abundance and assemblage composition of micronekton between offshore and nearshore locations. Each Cobb trawl tow was fished in a standardized fashion to make each sample comparable in terms of effort (as in Drazen et al., 2011). More specifically, each tow was rapidly lowered to the target depth, stabilized and towed for 1 h at the target depth. Haul back was also conducted rapidly and the ship was slowed during net shooting and haul back to reduce filtration in shallower

non-target layers. Despite this approach some capture of animals from surface waters will occur. However, previous tows in shallow nighttime waters using the same system in the same area off west Hawai'i show substantially different assemblages overwhelmingly dominated by high abundances of Myctophidae (50–70% of fish abundance and 70–80% of biomass; Drazen et al., 2011). Survey depth was monitored in real time (0.1m resolution, updated every 5 s) using a Marport net monitoring system. For day time 2017 trawls, survey depths ranged from 502 to 513 m, with a mean maximum depth of 508 m and 506 m at offshore and nearshore sites, respectively. During the 2017 night time trawls, offshore survey depths ranged from 501 to 563 m (mean maximum depth of 518 m) and nearshore survey depths ranged from 478 to 579 m (mean maximum depth of 541 m). Moon phase was assumed to not affect our results due to the deep depths of our trawls (Drazen et al., 2011).

On the ship, we sorted the micronekton into several broad taxonomic groups including fishes, cephalopods, crustaceans, gelatinous zooplankton, and zooplankton (trapped in the 1m plankton net which formed the back end of our sampling system). Gelatinous plankton were not quantitatively sampled and were discounted from further analysis. We counted and weighed the fishes, cephalopods, and crustaceans, but were only able to weigh, not count, the zooplankton due to their small size or our inability to differentiate between individuals. At the time of sorting all micronekton were fixed in 10% buffered formalin solution to preserve morphological features. The formalin preserved fishes were subsequently sorted to a family level, re-weighed, and counted in the laboratory post-cruise. Anglerfishes were rare and pooled into the suborder Ceratioidei. Juvenile shore fishes, which included many coral reef families, were also pooled. Astronesthinae and Chauliodontinae are subfamilies of the Stomiidae and distinct taxonomically so were retained separately in the analysis.

## 2.2. Data analyses

To compare the biomass and abundance between offshore and nearshore stations we used a permutational analysis of variance (PERMANOVA) (Anderson, 2001) using a Euclidian distance matrix for total biomass and total abundance. The same approach was used for the acoustic NASC values. We further compared the broad taxonomic groups: fishes, crustaceans, cephalopods and zooplankton (the latter for biomass only). Abundance and biomass of individual fish families was also performed in this manner for those identified by similarity percentages (SIMPER) analysis to have contributed significantly to dissimilarity in fish assemblages between stations.

Fishes comprised the majority of biomass and abundance so their assemblage composition was compared between stations at the family level. Data sets were first subjected to a dispersion-weighting pre-treatment (Clarke et al., 2006). This was done to 'down weight' the influence of a single dominant taxon or taxa displaying a low signal to noise ratio (i.e. dominant in a single replicate trawl but absent from others) that was observed in our data. The PERMANOVA tests were based on a Bray-Curtis similarity matrix, Type III (partial) sums-of-squares, and unrestricted permutations of the raw data. When the global model was significant, we visualized the patterns using non-metric multi-dimensional scaling (nMDS) and used SIMPER analysis to identify the taxa contributing at least 5% to the dissimilarity between nearshore and offshore locations. The SIMPER analysis also used a Bray-Curtis similarity matrix on the dispersion weighted data. All analyses were completed using the PERMANOVA + add-on for the PRIMER v7 software (Anderson et al., 2008).

## 3. Results

### 3.1. Patterns in biomass and abundance of mesopelagic micronekton

Micronekton acoustic backscatter in the deep scattering layer

(400–600 m) along the west coast of Hawai'i was consistently higher in the nearshore relative to the offshore in 2016 and 2017, at both 70 kHz (Figs. 1) and 38 kHz (Supp. Fig. 1). In 2016, the higher backscatter appeared to be shifted northward along the coast. Little offshore area (deeper than 2000m isobath) was sampled. In 2017 during the day, the maximum of 500 m mean 70 kHz acoustic NASC values nearshore was 1.9 times higher than that offshore (1566 and 816  $\text{m}^2 \text{nm}^{-2}$ , respectively). During the night in 2017, the maximum mean NASC values nearshore was 1.4 times higher than that offshore (1375 and 980  $\text{m}^2 \text{nm}^{-2}$ , respectively) (Fig. 1). We also compared mean 70 kHz NASC values (Fig. 2; 38 kHz in Supp. Fig. 2) and, due to diel migration, daytime values at this depth were higher than those in nighttime (PERMANOVA, pseudo-F = 446,  $p < 0.0001$ ). Nearshore NASC values were significantly higher than corresponding offshore values (PERMANOVA, pseudo-F = 660,  $p < 0.0001$ ) and this was the case for both day and night and in both years (PERMANOVA pair-wise tests, pseudo-F = 3.4 to 22.6,  $p < 0.001$  in all 4 cases). There were few data beyond the 2000m isobath in 2016 so the relatively higher daytime NASC values (Fig. 2) reflect values much closer to shore than during 2017 (Fig. 1), though they were still significantly lower than those nearshore (PERMANOVA pair-wise test, pseudo-F = 3.42,  $p < 0.01$ ).

Trawl-estimated micronekton total biomass and abundance were higher nearshore than offshore in the 450–550 m depth layer along the west coast of Hawai'i (Fig. 3). Total micronekton (fishes, crustaceans, and cephalopods) abundance in both years was 2.7 times higher nearshore than offshore (Fig. 3a; Pseudo- $F_{1,10} = 7.966$ ,  $p = 0.036$  for 2016; Pseudo- $F_{1,11} = 9.176$ ,  $p = 0.018$  for 2017). Mean ( $\pm$ SE) total night time micronekton biomass nearshore in 2017 was 2.2 times higher than that offshore (Fig. 3b; Pseudo- $F_{1,11} = 5.613$ ,  $p = 0.028$ ). In 2016 biomass was 1.3 times higher nearshore but the difference was not statistically significant (Pseudo- $F_{1,10} = 2.573$ ,  $p = 0.160$ ).

We also compared the abundances and biomasses of the dominant micronekton taxa, fishes, crustaceans and cephalopods inshore to offshore and in many cases nearshore abundances were higher. Cephalopod abundance was significantly higher (2.4 fold) nearshore in 2017 only (Pseudo- $F_{1,11} = 5.345$ ,  $p = 0.0475$ ). Cephalopod biomass was generally higher nearshore (Fig. 4b) but due to high variability between tows this difference was not significant. Crustacean abundance and biomass were not significantly different between stations in either year. Fishes dominated the trawl-captured micronekton representing an average of 87 and 73% of abundance and biomass, respectively (Fig. 4). Fish abundance was significantly higher nearshore in both years (Pseudo- $F_{1,10} = 7.993$ ,  $p = 0.035$ , Pseudo- $F_{1,11} = 9.022$ ,  $p = 0.016$ ) with 3.2 and 2.9 times higher abundance nearshore. Biomass was marginally, but not significantly, higher in both years (Pseudo- $F_{1,10} = 2.952$ ,  $p = 0.090$ , Pseudo- $F_{1,11} = 4.814$ ,  $p = 0.060$ ). In addition to the micronekton, zooplankton biomass was significantly higher nearshore versus offshore

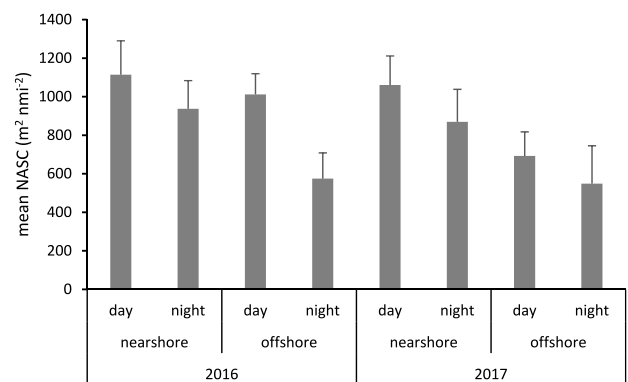
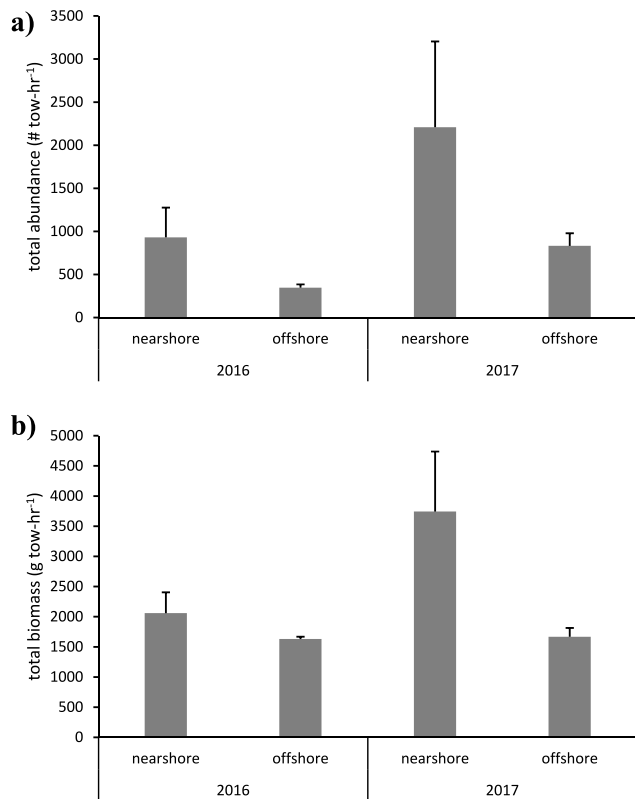


Fig. 2. Mean (with standard deviation) of 70 kHz acoustic NASC values in offshore and nearshore areas in 2016 and 2017. Values are presented for both day and night.



**Fig. 3.** a) Total abundance (number of organisms tow-hr<sup>-1</sup>) and b) biomass (g tow-hr<sup>-1</sup>) at night at offshore and nearshore locations in 2016 and 2017. Averages are shown in grey bars with standard deviation as whiskers.

both in 2016 (2.9 fold;  $71.6 \pm 26.1$  vs  $24.8 \pm 10.9$  g tow-hr<sup>-1</sup>; Pseudo- $F_{1,10} = 8.552$ ,  $p = 0.017$ ) and in 2017 (2.1 fold;  $243 \pm 105$  vs  $117 \pm 41.9$  g tow-hr<sup>-1</sup>; Pseudo- $F_{1,11} = 6.339$ ,  $p = 0.027$ ).

### 3.2. Patterns of micronekton assemblage composition

The assemblage composition of micronekton fishes differed between nearshore and offshore locations in both 2016 and 2017 for both abundance and biomass metrics (PERMANOVAs,  $p < 0.01$ ; Fig. 5). In 2016, the two locations had 45.6% dissimilarity, which was slightly lower, 37.4%, in 2017 based on abundances. In terms of biomass, the locations' fish assemblages were 41 and 42% dissimilar in 2016 and 2017, respectively. A relatively small number of taxa contributed substantially to these differences each representing >5% of the dissimilarity (Table 1; Supplementary Table 1; Supp. Fig. 4). Of these taxa, Serrivomeridae and Sternoptychidae abundance and biomass were consistently statistically higher nearshore in both years. The species that contributed most to the increased biomass was Serrivomeridae with 4-5x higher biomass nearshore. Myctophidae biomasses were relatively (but not statistically) higher nearshore in both years but abundance was statistically higher only in 2017. Biomass of Bregmacerotidae and Stylophoridae abundance, both somewhat uncommon taxa, were higher nearshore in 2017 (but not 2016), contributing to more than 5% of the dissimilarity. Setarchidae, which comprised the species *Ectreposebastes imus*, was only found in nearshore tows in both years but, it was captured sporadically so contributions to station dissimilarity were not high (Table 1). Taxa that contributed to assemblage dissimilarity and were more abundant or had greater biomass offshore were less consistent. Melamphaeidae abundances were statistically higher offshore in both years and biomass in 2016. Nemichthyidae abundance and biomass were statistically higher offshore in 2016. Anoplogasteridae, though

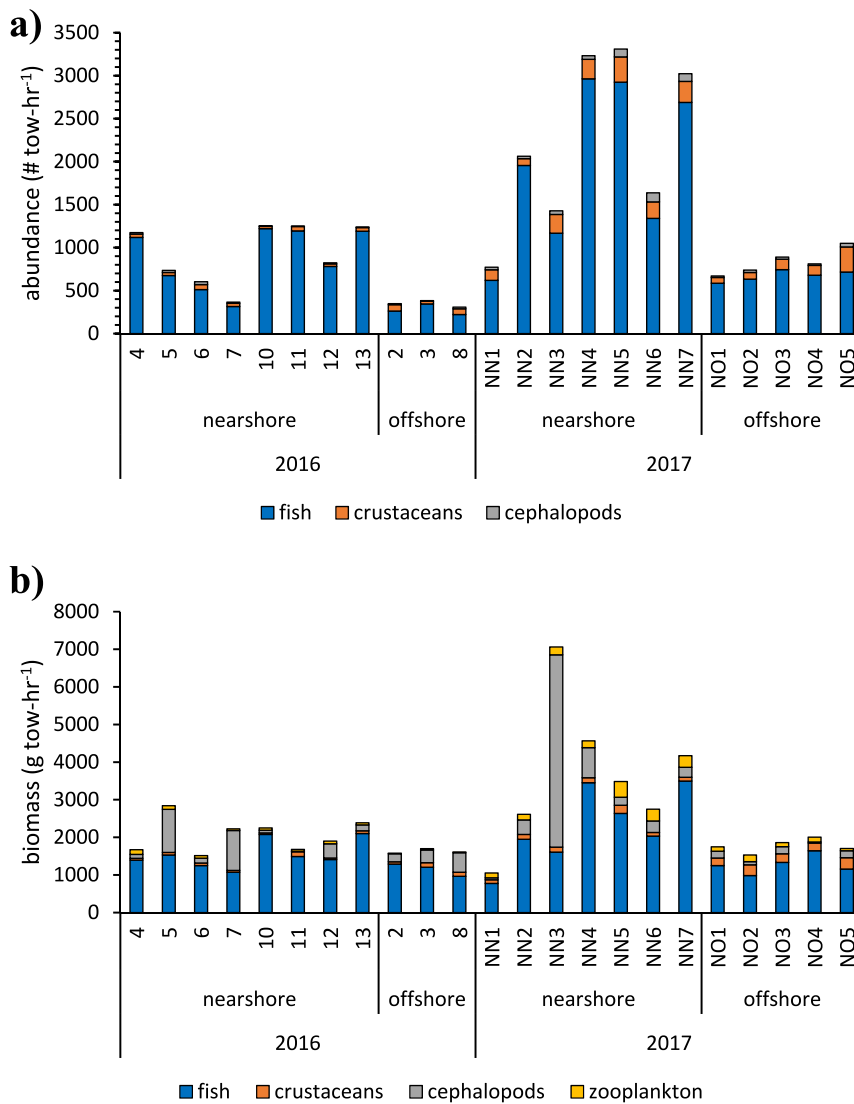
uncommon, contributed to dissimilarity and had statistically higher biomass offshore in 2016 (and was absent in the nearshore in both years). Juvenile shore fishes also had relatively higher biomass offshore in 2017. Gonostomatidae and Stomiidae were common, contributed to dissimilarity, and alternated the station where they were dominant between years. In 2016, Gonostomatidae abundance and biomass were relatively higher nearshore but in 2017 their biomass was relatively higher offshore. Also in 2016, Stomiidae abundance and biomass were relatively higher offshore but then were statistically higher nearshore in 2017.

## 4. Discussion

The enhancement of deep non-migratory mesopelagic micronekton along West Hawai'i was persistent over years, suggesting this was a regular ecological feature in the region. Abecassis et al. (2015) documented a higher nearshore acoustic biomass in 2011, 2013 and 2014 compared to offshore locations, and the results presented here extend this pattern to 2016 and 2017. This backscatter was elevated at 70 kHz but not as strongly at 38 kHz. This could mean that the backscatter came from smaller fishes or from fishes with smaller gasbladders (Kloser et al., 2002) or perhaps siphonophores. In reference to the latter, one study found a peak in siphonophore abundance in the epipelagic off Hawai'i (Steinberg et al., 2008) rather than at the depths we targeted but their abundance off west Hawaii is unknown. Our trawl results, concurrent with the acoustics, sampled these deep 70 kHz layers and confirmed that there is a 1.3 to 2.7-fold increase in abundance and biomass of micronekton nearshore compared to locations 24 km offshore. This was similar to the 2-fold increase in acoustic backscatter.

The differences in micronekton assemblages observed from trawl samples between the offshore and nearshore indicate that the nearshore assemblage was not simply higher abundances of the same offshore fauna in a nearshore environment. The nearshore assemblage consisted of reduced abundances or biomasses of some taxa such as the Melamphaeidae, Nemichthyidae and Anoplogasteridae and increased abundances and biomasses of others, such as the Serrivomeridae and Sternoptychidae (and Stomiidae in 2017). The two most consistently abundant nearshore taxa were non-migratory or weak migrators (Badcock and Baird, 1980; Barnett, 1983; van Utrecht and van Utrecht-Cock, 1987). In contrast, the Stomiidae do vertically migrate (Clarke, 1974). The offshore taxa have a range of migration patterns from deeper diel vertical migration in the Melamphaeidae, often not into the upper 200 m (Clarke, 1980; Clarke and Wagner, 1976), non-synchronous migrations in nemichthyid eels (Feagans-Bartow and Sutton, 2014; Gartner et al., 2008), or no migration (Anoplogasteridae (Clarke and Wagner, 1976). Finding that the taxa that differed significantly in abundance or biomass between locations were often non-migrating or weakly migrating species is not entirely surprising given we targeted mesopelagic depths during the night when most migrators have departed for shallower waters. What may be more important is that the presence of non-migratory or weakly migratory fishes in abundance nearshore, supports the consistent day and night peak of 70 kHz NASC at depth (Fig. 1; Abecassis et al., 2015). Though there is no other work close to shore off West Hawai'i, previous deep tows during the day about 18 km offshore of this coastline found a similar composition of the micronekton to that found here (Drazen et al., 2011). Total abundances were similar in the published data, as was the dominance of fishes including the Gonostomatidae. Tows integrating 0-1200m off leeward Oahu (10-25 km offshore) with a much finer meshed smaller net found *Cyclothone* spp., Penaidae, Myctophidae and Euphausidae to dominate abundance and Myctophidae, Caridea, Cephalopoda, and Anguilliformes to dominate biomass in that order (Maynard et al., 1975). Their composition is skewed towards smaller taxa (e.g. Euphausidae, *Cyclothone* spp.) and many more crustaceans that was found with the large Cobb trawl sampling described here.

The deep non-migratory micronekton assemblage we describe here



**Fig. 4.** a) Night time abundance (number of organisms tow-hr<sup>-1</sup>) and b) biomass (g tow-hr<sup>-1</sup>) of broad taxonomic groups offshore and nearshore from analysis of trawl data.

was different from the mostly migratory mesopelagic boundary layer (MBL) assemblage previously described in the Hawaiian Islands. Reid et al. (1991) describes evidence for 23 species of fishes, squids and crustaceans belonging to the island flank-associated mesopelagic micronekton assemblage, including two from studies farther up the island chain on seamounts (Boehlert et al., 1994; Wilson and Boehlert, 2004). These species were all found in great abundance over seafloor depths of less than 1000m but were either absent or less abundant farther offshore. Of the taxa identified, most undergo diel vertical migration or remain in close association with the seafloor such that they were captured in benthic trawls (Struhsaker, 1973) but not in midwater trawls towed a few hundred meters off the bottom. Though a more detailed taxonomic description of our nearshore fauna would be ideal, we can make some general comparisons to the MBL fauna. For instance, several migratory myctophids are important MBL species (Reid et al., 1991). Our myctophids may have been non-migrators (or at least non-migrating individuals) because we captured them at depth during the night but they could also have been contaminants from surface waters. We did find myctophid biomass (and abundance in 2017) was higher nearshore. These could represent some of the MBL assemblage, but other fishes dominated the nearshore assemblage we sampled. For

instance, the Serrivomeridae dominated our deep catches nearshore but are not MBL members. Several sternoptychids were classified as part of the MBL but these were mostly bottom trawled (*Argyripnus* spp. or *Polyipnus* spp.) or quite rare species (Reid et al., 1991). Though we did not identify our sternoptychids to species, all were *Argyropelecus* spp. or *Sternoptyx* spp. We did not capture the distinctive *Argyripnus* spp. or *Polyipnus* spp. which is not surprising given our tows occurred well off the seafloor at about the 1000m isobath. We captured the setarchid, *Ectreposebastes imus*, in a few nearshore stations and never offshore, which is a similar situation to Reid et al.'s (1991) trawling data. As a result Reid et al. (1991) did not consider it an MBL species but postulated that *E. imus* may be benthic during the day and migrate off the bottom at night along the island slopes.

The mechanism(s) driving nearshore enhancements of both MBL and non-migratory deep scattering layer micronekton assemblages remain poorly understood. Why do these assemblages exist along island slopes? The MBL migrates inshore, some species even into very shallow water over reefs (Benoit-Bird et al., 2001), where they likely take advantage of trophic subsidies from the Island Mass Effect supported phytoplankton and zooplankton production (Benoit-Bird and McManus, 2012). Increased macroplankton and micronekton biomass in surface waters off

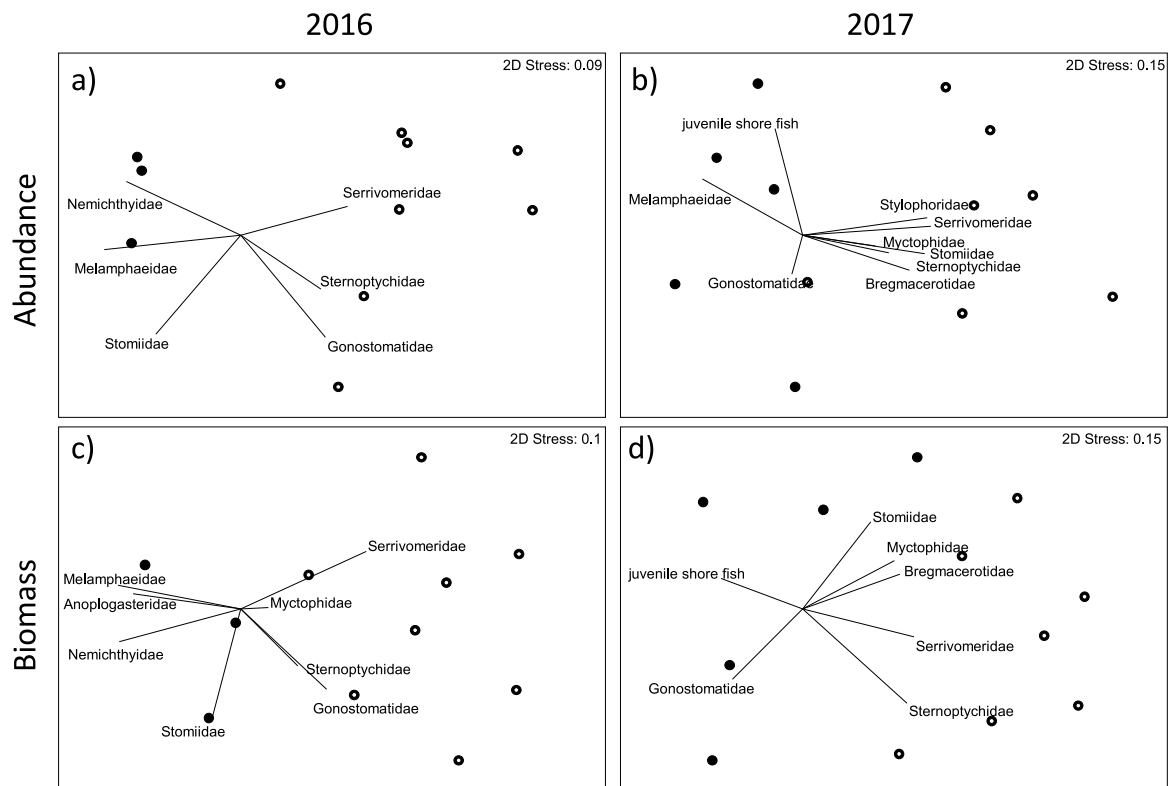


Fig. 5. Variations in assemblage patterns of fishes at a family level between the night time offshore (solid symbols) and nearshore (open symbols). a) 2016 abundance, b) 2017 abundance, c) 2016 biomass and d) 2017 biomass. Those fish families identified by SIMPER analysis to be driving site differences are overlaid as a bi-plot, with the length of the vector proportional to the strength of the correlation with the ordination axes.

Guam have been attributed to Island Mass Effect related production (Suntsov and Domokos, 2013). Previous research has shown that the island of Hawai'i has a phytoplankton biomass 30% higher than offshore of the island (Gove et al., 2016). Across both study years there was a greater biomass of zooplankton, composed mostly of krill. Previous diet work does suggest that smaller serrivomerids and sternoptychids predate upon crustaceans including krill (Clarke, 1984; Geidner, 2008; Ridge-Cooney, 1987). Serrivomeridae accounted for the largest biomass and abundance of any one family in nearshore locations (Table 1). The finding of higher densities of zooplankton/krill, and some micronekton is suggestive of bottom-up IME type processes, however, rates of production and locally confirmed trophic links between taxa would also be required to prove this hypothesis. It may also be worthwhile to evaluate changes in the size of primary producers as larger ones could shorten food-webs and funnel more production to higher trophic levels (Ryther, 1969; Woodworth-Jefcoats et al., 2012). Importantly, it remains to be seen if non-migratory or weakly migratory taxa take advantage of the MBL that feed nearshore in shallow water at night by consuming them when they migrate to depth during the day. It is certainly possible as the daytime depths of the MBL are from 400 to 700m (Reid et al., 1991).

It is also possible that the nearshore mesopelagic micronekton enhancement derives from processes other than bottom up trophic forcing. The West Hawai'i coast lies in the lee of the island of Hawai'i with the North Equatorial Current to the south of the island and the North Hawaiian Ridge Current on the north end of the island, both flowing generally to the west (Lumpkin, 1998; Qiu et al., 1997). Furthermore, the lee of the island is the site of cyclonic/anticyclonic mid-ocean eddy formation (Calil et al., 2008) which can act to advect surface ichthyoplankton closer to shore or retain them nearshore (Lindo-Atichati et al., 2020; Lobel and Robinson, 1988) and may concentrate micronekton (Drazen et al., 2011). With such a complicated flow regime, we cannot dismiss the hypothesis that advection concentrates

plankton in the current lee of Hawai'i island and results in dense micronekton assemblages. Alternatively, if deeper flows also result in convergence at depth it is possible that less mobile micronekton, like in the deep non-migratory layers, might also be advected and concentrated there. Similarly, increases in acoustic and trawl estimated macrozooplankton and micronekton occur in the current lee of the Prince Edward Islands, though the exact mechanisms remain elusive (Pakhomov and Froneman, 1999). Evaluation of advective hypotheses off West Hawai'i will require high resolution measurements of the flow regime at the depths of these layers to compare to more systematic mapping of the micronekton enhancement.

We have documented the occurrence of a temporally persistent, high abundance, largely non-migratory layer of mesopelagic micronekton in the nearshore West Hawai'i ecosystem. This assemblage is described for the first time. It differs significantly from that found offshore at similar depths and from the better known mostly migratory MBL assemblage (Benoit-Bird et al., 2001; Reid et al., 1991). It seems possible that this assemblage derives from the Island Mass Effect, though other mechanisms such as advection and passive concentration could exist. These enhancements may help explain the high abundance of marine mammals and pelagic fishes off the coast (Abecassis et al., 2015). For instance, *Serrivomer beanii* was the most common fish species ingested by pygmy sperm whales in Hawai'i (West et al., 2009) and serrivomerids were the most abundant nearshore taxon in our trawl catches. Cephalopods are also very important prey to these marine mammals but they are notoriously difficult to capture in trawls and variability in our data prevented us from coming to any strong conclusions about their importance to the nearshore acoustic scattering layer.

An important next step will be to more comprehensively map the acoustic biomass and utilize depth-discrete net tows to more finely resolve depth and lateral changes in assemblage composition. Better information on the spatial characteristics of the assemblage could be

**Table 1**

Mean ( $\pm$  1SD) biomass (g tow-hr<sup>-1</sup>) and abundance (number tow-hr<sup>-1</sup>) of all fishes collected at night time off the west coast of Hawai'i in 2016 and 2017. Numbers in parentheses are sample sizes. Values in bold are those taxa which contributed to >5% of the dissimilarity between nearshore and offshore fish assemblages (SIMPER) and those with higher mean abundances or biomasses are shaded in gray. An asterisk indicates a statistically higher mean abundance or biomass (PERMANOVA, p<0.05).

Family	2016				2017			
	Offshore (3)		Nearshore (8)		Offshore (5)		Nearshore (7)	
	Biomass (g tow-hr <sup>-1</sup> )	Abundance (# tow-hr <sup>-1</sup> )	Biomass (g tow-hr <sup>-1</sup> )	Abundance (# tow-hr <sup>-1</sup> )	Biomass (g tow-hr <sup>-1</sup> )	Abundance (# tow-hr <sup>-1</sup> )	Biomass (g tow-hr <sup>-1</sup> )	Abundance (# tow-hr <sup>-1</sup> )
Anoplogasteridae	<b>54.1 ± 35.2*</b>	2 ± 0	<b>0</b>	0	9.2 ± 20.6	0.4 ± 0.9	0	0
Astronesthinae	13.1 ± 22.7	0.3 ± 0.6	34.8 ± 46.1	1.1 ± 1.4	50.5 ± 113	0.2 ± 0.4	0	0
Bathylagidae	0	0	0	0	0	0	4.8 ± 8.2	0.3 ± 0.5
Bregmacerotidae	0.5 ± 0.5	0.7 ± 0.6	0.8 ± 1.3	0.8 ± 1	<b>1.3 ± 0.9</b>	<b>1.4 ± 1.1</b>	<b>4.9 ± 4</b>	<b>3.7 ± 2.0</b>
Ceratioidei	8.3 ± 13.6	0.7 ± 0.6	0 ± 0	0 ± 0	0.4 ± 0.9	0.2 ± 0.4	3.8 ± 6.7	0.4 ± 0.5
Cetomimidae	4.2 ± 7.3	0.3 ± 0.6	0 ± 0	0 ± 0	2.7 ± 6	a0.2 ± 0.4	1.1 ± 2.9	0.1 ± 0.4
Chauliodontinae	64.9 ± 88.6	3 ± 2.6	11.5 ± 15.3	0.5 ± 0.5	2.6 ± 4.5	0.6 ± 0.9	5.9 ± 15.6	0.3 ± 0.8
Chiasmodontidae	5.4 ± 6.5	0.7 ± 0.6	0	0	4 ± 7.5	0.6 ± 0.9	0	0
Derichthyidae	0	0	0.3 ± 0.5	0.3 ± 0.5	0	0	0	0
Evermannellidae	1.6 ± 2.7	0.3 ± 0.6	1.3 ± 3.5	0.3 ± 0.7	4.1 ± 6.7	0.8 ± 1.3	0.7 ± 1.8	0.1 ± 0.4
Giganturidae	1.7 ± 1.5	1.3 ± 1.5	3.2 ± 3	1.6 ± 1.5	0	0	0	0
Gonostomatidae	<b>295.4 ± 102.6</b>	<b>66.3 ± 16.9</b>	<b>368.8 ± 109.3</b>	<b>108.5 ± 33.7</b>	<b>397.7 ± 194.4</b>	<b>115.8 ± 35.6</b>	<b>293.3 ± 80.5</b>	<b>112 ± 34.7</b>
Howellidae	3.1 ± 5.4	0.3 ± 0.6	0	0	3.3 ± 4.6	0.4 ± 0.5	7.1 ± 9.7	1.1 ± 1.2
juvenile shore fish	2.5 ± 2.2	5.3 ± 2.1	5.9 ± 6.3	5.5 ± 6.2	<b>42.5 ± 40.1</b>	73.6 ± 31.4	<b>18.2 ± 6.9</b>	70.9 ± 31.1
Macrouridae	0	0	4.5 ± 12.9	0.1 ± 0.4	0	0	0	0
Melamphaeidae	<b>168.7 ± 56.9*</b>	<b>14.7 ± 0.6*</b>	<b>37.4 ± 30.7</b>	<b>2.4 ± 2.1</b>	84.5 ± 37.9	<b>10.8 ± 4.9*</b>	37.3 ± 62.2	<b>2.4 ± 2.6</b>
Melanonidae	14.5 ± 19.2	1.3 ± 1.2	43.5 ± 45.6	1.3 ± 1	0	0	8.6 ± 16.8	0.3 ± 0.5
Myctophidae	<b>64.6 ± 28.3</b>	49.7 ± 15.6	<b>74.7 ± 32.2</b>	59.4 ± 31.5	<b>259.2 ± 66.5</b>	<b>241.6 ± 65.8</b>	<b>309.4 ± 116</b>	<b>293.3 ± 92.3</b>
Nemichthyidae	<b>98 ± 24.1*</b>	<b>12.3 ± 0.6*</b>	<b>47 ± 23.2</b>	<b>6.9 ± 3.2</b>	12.8 ± 10.6	2 ± 1.4	22.7 ± 21.8	3.4 ± 3.1
Neoscopelidae	30.6 ± 53.1	0.7 ± 1.2	0	0	0	0	0	0
Notosudidae	0	0	15 ± 41.4	0.3 ± 0.5	2.1 ± 4.2	1 ± 1.2	1.2 ± 1	1.3 ± 1.3
Ophidiidae	1.3 ± 2.3	0	0 ± 0	0	0	0	61 ± 161.4	0.1 ± 0.4
Opisthoproctidae	24.2 ± 23.8	3 ± 2.6	26.2 ± 29.6	3.1 ± 4.1	22.8 ± 21.1	2.4 ± 1.5	18.1 ± 14.6	2.7 ± 2.1
Paralepididae	0	0	0	0	0.2 ± 0.4	8.4 ± 18.8	1.3 ± 2.1	1.3 ± 1.8
Scombrobracidae	0	0	0	0	0	0	5.3 ± 14.1	0.1 ± 0.4
Scopelarchidae	0	0	1.5 ± 2.7	0.3 ± 0.5	12 ± 22.9	0.4 ± 0.5	12.7 ± 14.3	0.7 ± 1.1
Serrivomeridae	<b>118.6 ± 124.8</b>	<b>64.7 ± 79.9</b>	<b>636.8 ± 258.6*</b>	<b>629.1 ± 377.5*</b>	<b>239.3 ± 43.9</b>	<b>182.6 ± 41.6</b>	<b>1257.1 ± 738.9*</b>	<b>1393.3 ± 892.6*</b>
Setarchidae	0	0	32.7 ± 37.1	0.9 ± 1	0	0	38.7 ± 55.1	0.7 ± 0.8
Sternoptychidae	<b>30.6 ± 17.8</b>	<b>6.0 ± 2.6</b>	<b>55.1 ± 24.1</b>	<b>21.4 ± 10.6*</b>	<b>10.6 ± 7.3</b>	<b>6.0 ± 3</b>	<b>36.7 ± 14.4*</b>	<b>15 ± 7.9*</b>
Stomiidae	<b>128.7 ± 14</b>	<b>34.7 ± 12.9</b>	<b>103.9 ± 49.3</b>	<b>25.5 ± 9.1</b>	<b>109.7 ± 76.4</b>	<b>21.4 ± 6.8</b>	<b>122.6 ± 31.8</b>	<b>42.9 ± 16.8*</b>
Stylophoridae	0.7 ± 1.2	0.7 ± 1.2	5 ± 9.4	0.5 ± 0.9	2.6 ± 5.3	<b>0.6 ± 0.9</b>	4.9 ± 2.8	<b>4.4 ± 2.1*</b>
Trachipteridae	11.6 ± 20.1	0.3 ± 0.6	0	0	0	0	0	0
Trichiuridae	0	0	25.3 ± 71.5	0.3 ± 0.5	0	0	0	0

compared more precisely to the distribution of primary production, bathymetry, and current regimes in the lee of Hawai'i Island. These comparisons could help elucidate causal mechanisms and lead to predictions about where other micronekton enhancements are likely to occur in Hawai'i and in other archipelagos. Future work could also focus on comparing these results to other regions without such strong Island Mass Effect, and perhaps use trophic tracers to identify if nearshore primary production is indeed an important trophic input to the micronekton assemblage. In our changing world, the importance of understanding the connections between seemingly distant habitats, such as nearshore reefs and the mesopelagic, is of critical importance and could change our views about the ocean as an interconnected ecosystem.

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**Ethics approval**

Sampling was done under the approval of the National Oceanic and Atmospheric Administration.

**Authors contributions**

JMG, JCD, and GJW conceived and designed the research; BC, JCD, JEP, JMG, AC, DRK, and JW collected the data; JCD, BC and GJW analysed the data; JCD and GJW wrote the manuscript with BC and JMG, and all authors contributed to revisions.



## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Data availability

Data will be made available on request.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.dsr.2023.104107>.

## References

- Abecassis, M., Polovina, J., Baird, R.W., Copeland, A., Drazen, J.C., Domokos, R., Oleson, E., Jia, Y., Schorr, G.S., Webster, D.L., Andrews, R.D., 2015. Characterizing a foraging hotspot for short-finned pilot whales and Blainville's beaked whales off the west side of the Island of Hawai'i with tagging and oceanographic data. *PLoS One* 10 (11), e0142628.
- Anderson, M.J., 2001. A new method for non-parametric multivariate analysis of variance. *Austral Ecol.* 26 (1), 32–46.
- Anderson, M.J., Gorley, R.N., Clarke, K.R., 2008. PERMANOVA+ for PRIMER: Guide to Software and Statistical Methods. PRIMER-E Ltd, Plymouth, UK.
- Ariza, A., Garjo, J., Landeira, J., Bordes, F., Hernández-León, S., 2015. Migrant biomass and respiratory carbon flux by zooplankton and micronekton in the subtropical northeast Atlantic Ocean (Canary Islands). *Prog. Oceanogr.* 134, 330–342.
- Badcock, J., Baird, R.C., 1980. Remarks on systematics, development, and distribution of the hatchetfish genus *Sternoptyx* (Pisces, Stomiatoidei). *Fish. Bull.* 77, 803–820.
- Barnett, M.A., 1983. Species structure and temporal stability of mesopelagic fish assemblages in the central Gyres of the North and South Pacific Ocean. *Mar. Biol.* 74 (3), 245–256.
- Benoit-Bird, K.J., Au, W.W.L., Brainard, R.E., Lammers, M.O., 2001. Diel horizontal migration of the Hawaiian mesopelagic boundary community observed acoustically. *Mar. Ecol. Prog. Ser.* 217, 1–14.
- Benoit-Bird, K.J., McManus, M.A., 2012. Bottom-up regulation of a pelagic community through spatial aggregations. *Biol. Lett.* 8 (5), 813–816.
- Bertrand, A., Bard, F.X., Josse, E., 2002. Tuna food habits related to the micronekton distribution in French Polynesia. *Mar. Biol.* 140 (5), 1023–1037.
- Boehlert, G.W., Wilson, C.D., Mizuno, K., 1994. Populations of the sternoptychid fish *Maurolucus muelleri* on seamounts in the Central North Pacific. *Pac. Sci.* 48 (1), 57–69.
- Brodeur, R.D., Yamamura, O. (Eds.), 2005. Micronekton of the North Pacific. PICES Scientific Report No. 30. North Pacific Marine Science Organization (PICES).
- Calil, P.H.R., Richards, K.J., Jia, Y., Bidigare, R.R., 2008. Eddy activity in the lee of the Hawaiian Islands. *Deep Sea Res. Part II Top. Stud. Oceanogr.* 55 (10–13), 1179.
- Cascão, I., Domokos, R., Lammers, M.O., Marques, V., Domínguez, R., Santos, R.S., Silva, M.A., 2017. Persistent enhancement of micronekton backscatter at the summits of seamounts in the Azores. *Front. Mar. Sci.* 4 (25).
- Catul, V., Gauns, M., Karuppasamy, P.K., 2011. A review on mesopelagic fishes belonging to family Myctophidae. *Rev. Fish Biol. Fish.* 21 (3), 339–354.
- Choy, C.A., Wabnitz, C.C.C., Weijerman, M., Woodworth-Jefcoats, P.A., Polovina, J.J., 2016. Finding the way to the top: how the composition of oceanic mid-trophic micronekton groups determines apex predator biomass in the central North Pacific. *Mar. Ecol. Prog. Ser.* 549, 9–25.
- Clarke, K.R., Chapman, M.G., Somerfield, P.J., Needham, H.R., 2006. Dispersion-based weighting of species counts in assemblage analyses. *Mar. Ecol. Prog. Ser.* 320, 11–27.
- Christiansen, B., Martin, B., Hirsch, S., 2009. The benthopelagic fish fauna on the summit of Seine Seamount, NE Atlantic: composition, population structure and diets. *Deep Sea Res. Part II Top. Stud. Oceanogr.* 56 (25), 2705–2712.
- Clarke, T.A., 1974. Some aspects of the ecology of Stomiatioid fishes in the Pacific Ocean near Hawaii. *Fish. Bull.* 72, 337–351.
- Clarke, T.A., 1980. Diets of fourteen species of vertically migrating mesopelagic fishes in Hawaiian waters. *Fish. Bull.* 78 (3), 619–640.
- Clarke, T.A., 1984. Ecology and sexual dimorphism of the pelagic eel, *Stemonidium hypomelas* (Serrivomeridae). *Copeia* (1), 249–252.
- Clarke, T.A., Wagner, P.J., 1976. Vertical distribution and other aspects of the ecology of certain mesopelagic fishes taken near Hawaii. *Fish. Bull.* 74 (3), 635–645.
- Davison, P.C., Checkley Jr., D.M., Koslow, J.A., Barlow, J., 2013. Carbon export mediated by mesopelagic fishes in the northeast Pacific Ocean. *Prog. Oceanogr.* 116 (0), 14–30.
- De Forest, L.G., Drazen, J.C., 2009. The influence of a Hawaiian seamount on mesopelagic micronekton. *Deep Sea Res. I* 56, 232–250.
- Demer, D.A., Berger, L., Bernasconi, M., Bethke, E., Boswell, K., Chu, D., Domokos, R., Dunford, A., Fassler, S., Gauthier, S., 2015. Calibration of acoustic instruments. *ICES (Int. Counc. Explor. Sea) Coop. Res. Rep.* 326, 1–133.
- Dornan, T., Fielding, S., Saunders, R.A., Genner, M.J., 2019. Swimbladder morphology masks Southern Ocean mesopelagic fish biomass. *Proc. Biol. Sci.* 286 (1903), 20190353.
- Doty, M.S., Oguri, M., 1956. The Island Mass Effect. *Journal du Conseil* 22, 33–37.
- Drazen, J.C., De Forest, L.G., Domokos, R., 2011. Micronekton abundance and biomass in Hawaiian waters as influenced by seamounts, eddies, and the moon. *Deep-Sea Res. I* 58, 557–566.
- Feagans-Bartow, J.N., Sutton, T.T., 2014. Ecology of the oceanic rim: pelagic eels as key ecosystem components. *Mar. Ecol. Prog. Ser.* 502, 257–266.
- Foote, K., Vestnes, G., MacLennan, D., Simmonds, E., 1987. Calibration of acoustic instruments for fish density estimation: a practical guide. *ICES (Int. Counc. Explor. Sea) Coop. Res. Rep.* 144, 1–81.
- Gartner, J.V., Sulak, K.J., Ross, S.W., Necaie, A.M., 2008. Persistent near-bottom aggregations of mesopelagic animals along the North Carolina and Virginia continental slopes. *Mar. Biol.* 153, 825–841.
- Geidner, M.E., 2008. Spatial and Trophic Ecology of the Sawtooth Eel, *Serrivomer Beanii*, a Biomass-Dominant Bathypelagic Fish over the Northern Mid-Atlantic Ridge.
- Genin, A., 2004. Bio-physical coupling in the formation of zooplankton and fish aggregations over abrupt topographies. *J. Mar. Syst.* 50 (1–2), 3–20.
- Gove, J.M., McManus, M.A., Neuheimer, A.B., Polovina, J.J., Drazen, J.C., Smith, C.R., Merrifield, M.A., Freidlander, A.M., Ehses, J.S., Young, C., Dillon, A.K., Williams, G. J., 2016. Ocean oases: near-island biological hotspots in barren ocean basins. *Nat. Commun.* 7, 10581.
- Hays, G.C., 2003. A review of the adaptive significance and ecosystem consequences of zooplankton diel vertical migrations. *Hydrobiologia* 503, 163–170.
- Klevjer, T.A., Irigoien, X., Røstad, A., Fraile-Nuez, E., Benítez-Barrios, V.M., Kaartvedt, S., 2016. Large scale patterns in vertical distribution and behaviour of mesopelagic scattering layers. *Sci. Rep.* 6 (1), 19873.
- Kloser, R.J., Ryan, T., Sakov, P., Williams, A., Koslow, J.A., 2002. Species identification in deep water using multiple acoustic frequencies. *Can. J. Fish. Aquat. Sci.* 59 (6), 1065–1077.
- Leitner, A.B., Neuheimer, A.B., Drazen, J.C., 2020. Evidence for long-term seamount-induced chlorophyll enhancements. *Sci. Rep.* 10 (1), 12729.
- Lindo-Atichati, D., Jia, Y., Wren, J.L.K., Antoniadou, A., Kobayashi, D.R., 2020. Eddies in the Hawaiian Archipelago region: formation, characterization, and potential implications on larval retention of reef fish. *J. Geophys. Res.: Oceans* 125 (5), e2019JC015348.
- Lobel, P.S., Robinson, A.R., 1988. Larval fishes and zooplankton in a cyclonic eddy in Hawaiian waters. *J. Plankton Res.* 10 (6), 1209–1223.
- Lumpkin, C.F., 1998. Eddies and Currents of the Hawaiian Islands. PhD, University of Hawaii.
- MacLennan, D., Simmonds, E., 1992. Fisheries Acoustics. Chapman and Hall.
- Maynard, S.D., Riggs, F.V., Walters, C.F., 1975. Mesopelagic micronekton faunal composition, standing stock, and diel vertical migration. *Fish. Bull.* 73, 726–736.
- Morato, T., Hoyle, S.D., Allain, V., Nicol, S.J., 2010. Tuna longline fishing around west and central Pacific seamounts. *PLoS One* 5 (12), e14453.
- Pakhomov, E.A., Froneman, P.W., 1999. Macroplankton/micronekton dynamics in the vicinity of the Prince Edward Islands (Southern Ocean). *Mar. Biol.* 134 (3), 501–515.
- Pauly, D., Piroddi, C., Hood, L., Bailly, N., Chu, E., Lam, V., Pakhomov, E.A., Pshenichnov, L.K., Radchenko, V.I., Palomares, M.L.D., 2021. The biology of mesopelagic fishes and their catches (1950–2018) by commercial and experimental fisheries. *J. Mar. Sci. Eng.* 9 (10), 1057.
- Perelman, J.N., Firing, E., van der Grient, J.M.A., Jones, B.A., Drazen, J.C., 2021. Mesopelagic scattering layer behaviors across the Clarion-Clipperton Zone: implications for deep-sea mining. *Front. Mar. Sci.* 8 (492), 632764.
- Porteiro, F.M., Sutton, T.T., 2007. Midwater fish assemblages and seamounts. In: Pitcher, T.J., Morato, T., Hart, P.J.B., Clark, M.R., Haggan, N., Santos, R.S. (Eds.), *Seamounts: Ecology, Fisheries and Conservation*. Blackwell Publishing, Oxford, pp. 101–116.
- Proud, R., Cox, M.J., Brierley, A.S., 2017. Biogeography of the global ocean's mesopelagic zone. *Curr. Biol.* 27 (1), 113–119.
- Qiu, B., Koh, D.A., Lumpkin, C., Flament, P., 1997. Existence and formation mechanism of the North Hawaiian Ridge Current. *J. Phys. Oceanogr.* 27 (3), 431–444.
- Reid, S.B., Hirota, J., Young, R.E., Hallacher, L.E., 1991. Mesopelagic-boundary community in Hawaii: micronekton at the interface between neritic and oceanic ecosystems. *Mar. Biol.* 109 (3), 427–440.

- Ridge-Cooney, V.L., 1987. Aspects of the Biology of Hatchetfishes (Family Sternoptychidae) in the Pacific Ocean Near Hawaii. Ph.D., University of Hawaii.
- Rogers, A.D., 2018. The biology of seamounts: 25 Years on. In: Sheppard, C. (Ed.), *Advances in Marine Biology*. Academic Press, pp. 137–224.
- Ryther, J.H., 1969. Photosynthesis and fish production in the sea. *Science* 166 (3901), 72–76.
- Saba, G.K., Burd, A.B., Dunne, J.P., Hernández-León, S., Martin, A.H., Rose, K.A., Salisbury, J., Steinberg, D.K., Trueman, C.N., Wilson, R.W., Wilson, S.E., 2021. Toward a better understanding of fish-based contribution to ocean carbon flux. *Limnol. Oceanogr.* 66 (5), 1639–1664.
- Seki, M.P., Lumpkin, R., Flament, P., 2002. Hawaii cyclonic eddies and blue Marlin catches: the case study of the 1995 Hawaiian International Billfish Tournament. *J. Oceanogr.* 58, 739–745.
- St John, M.A., Borja, A., Chust, G., Heath, M., Grigorov, I., Mariani, P., Martin, A.P., Santos, R.S., 2016. A dark hole in our understanding of marine ecosystems and their services: perspectives from the mesopelagic community. *Front. Mar. Sci.* 3 (31).
- Steinberg, D.K., Cope, J.S., Wilson, S.E., Kobari, T., 2008. A comparison of mesopelagic mesozooplankton community structure in the subtropical and subarctic North Pacific Ocean. *Deep Sea Res. Part II Top. Stud. Oceanogr.* 55 (14–15), 1615–1635.
- Struhsaker, P.J., 1973. A Contribution to the Systematics and Ecology of Hawaiian Bathyal Fishes. PhD, University of Hawaii, Honolulu.
- Suntsov, A., Domokos, R., 2013. Vertically migrating micronekton and macrozooplankton communities around Guam and the Northern Mariana Islands. *Deep Sea Res. Oceanogr. Res. Pap.* 71, 113–129.
- van Haren, H., Compton, T.J., 2013. Diel vertical migration in deep sea plankton is finely tuned to latitudinal and seasonal day length. *PLoS One* 8 (5), e64435.
- van Utrecht, W.L., van Utrecht-Cock, C.N., 1987. *Serrivomer beani* Gill & Ryder, 1884 (Pisces, Anguilliformes, Serrivomeridae): some aspects of seasonal variation in numbers and distribution in the mid North Atlantic. *Bijdr. Dierkd.* 57 (1), 53–58.
- West, K.L., Walker, W.A., Baird, R.W., White, W., Levine, G., Brown, E., Schofield, D., 2009. Diet of pygmy sperm whales (*Kogia breviceps*) in the Hawaiian Archipelago. *Mar. Mamm. Sci.* 25 (4), 931–943.
- Wilson, C.D., Boehlert, G.W., 2004. Interaction of ocean currents and resident micronekton at a seamount in the central North Pacific. *J. Mar. Syst.* 50, 39–60.
- Woodworth-Jefcoats, P.A., Polovina, J.J., Dunne, J.P., Blanchard, J.L., 2012. Ecosystem size structure response to 21st century climate projection: large fish abundance decreases in the central North Pacific and increases in the California Current. *Global Change Biol.* 19 (3), 724–733.