



Contents lists available at ScienceDirect

Deep-Sea Research I

journal homepage: www.elsevier.com/locate/dsrI

The influence of a Hawaiian seamount on mesopelagic micronekton

Lisa De Forest*, Jeffrey Drazen

Department of Oceanography, University of Hawaii, 1000 Pope Road, Honolulu, HI 96822 USA

ARTICLE INFO

Article history:

Received 19 March 2008

Received in revised form

2 September 2008

Accepted 17 September 2008

Available online 10 October 2008

Keywords:

Mesopelagic micronekton

Seamount

Hawaii

Myctophidae

Cephalopod

Shrimp

ABSTRACT

The distribution of mesopelagic micronekton (small fishes, crustaceans, and cephalopods) is not uniform throughout the oceans. Seamounts are a feature that may influence the abundance, biomass, diversity, and taxonomic composition of a community of mesopelagic micronekton by introducing a hard substrate and benthic predators into a realm normally devoid of these. Cross Seamount, located roughly 295 km south of the island of Oahu, Hawaii, has a summit that is 330 m below sea surface and has a diameter of approximately 8 km. Using a large, modified Cobb trawl, samples were taken both directly over and away from the summit of Cross Seamount to sample the deep scattering layer during the day and the shallow scattering layer during the night. Trawls were conducted during two cruises in the spring of 2005 and 2007. All organisms collected were identified to the lowest taxonomic level possible resulting in a description of the local assemblage of mesopelagic micronekton over and around Cross Seamount. Results indicate that there is a significant decrease in total abundance of organisms and an absence of certain diel vertically migrating taxa directly over the summit as opposed to away. While predation might be partly the cause, the taxa that are absent from the summit all have daytime depths that are deeper than the depth of the summit indicating that avoidance may be a major reason for the low abundance. The overall taxonomic composition of the community over the summit is dominated numerically by epipelagic juvenile fishes and stomatopod larvae. This is in opposition to that found away from the summit where the community is dominated numerically by mesopelagic fishes, mostly myctophid fishes, with the epipelagic juvenile fishes and stomatopod larvae contributing little to the overall taxonomic composition. The community over the summit also contains two species that appear to be found in higher abundance over the summit as opposed to away and may be considered as seamount-associated species. These are a cranchiid squid, *Liocranchia reinhardti*, and a myctophid fish, *Benthosema fibulatum*. This seamount is known to impact the mesopelagic micronekton community and tuna community, but the mechanisms behind these impacts are largely unknown at this time.

© 2008 Elsevier Ltd. All rights reserved.

1. Introduction

Mesopelagic micronekton are organisms generally between 2 and 20 cm in size and include such diverse

taxonomic groups as crustaceans, fishes, and cephalopods (Brodeur and Yamamura, 2005). This group of organisms is considered to be important in transferring the energy created by epipelagic primary and secondary production. This transfer of energy can be either to higher trophic levels, as mesopelagic micronekton are an important food source for many marine predators, or to the deeper regions of the ocean via respiration, excretion, and natural mortality while the mesopelagic micronekton are at depth

* Corresponding author.

E-mail addresses: lisadf@hawaii.edu, seacatch@gmail.com (L. De Forest).

(Pauly et al., 1998; Hidaka et al., 2001; Karpouzi et al., 2007). A characteristic of all mesopelagic micronekton is the ability to maintain a position and swim against currents with many undergoing diel vertical migration (Brodeur and Yamamura, 2005). Because of this characteristic, their distribution in the ocean is not dictated solely by passive drifting due to physical forces but also by behavior. Certain shallow features in the oceans, such as continental slopes, banks, and shelf-edges, may influence their abundance or community structure by altering the oceanic environment (Brodeur and Yamamura, 2005). This alteration could serve either to increase or decrease the abundance of these organisms. Due to the importance of these organisms as a food source for many marine predators, this change in abundance could also impact the abundance and distribution of marine predators over and around certain features.

Seamounts are another shallow feature in the ocean that may influence mesopelagic micronekton abundance and distribution. Seamounts are defined as isolated submarine mountains that have an elevation more than 1000 m above the seafloor with most being of volcanic origin (Rogers, 1994; Genin, 2004). There are approximately 30,000 such features rising at least 1000 m above the seafloor in the Pacific alone, making seamounts a relatively common feature in the oceans (Smith and Jordan, 1988). By projecting at least 1000 m into the water column, seamounts can generate a variety of impacts on physical flow regimes, mostly by influencing and changing existing tidal currents, thus creating a unique and different environment as opposed to the open ocean (Genin et al., 1989; Noble and Mullineaux, 1989; Mullineaux and Mills, 1997; Mohn and Beckmann, 2002). This could influence the abundance and distribution of mesopelagic micronekton. However, not all seamounts will generate the same effects. This is due to their different sizes, shapes, depths of the summit below sea surface, and distance from other seamount or bathymetric features (Porteiro and Sutton, 2007).

Changes in physical flow regimes around seamounts can potentially increase the amount of primary production in water either directly above or immediately downstream of seamounts (Boehlert and Genin, 1987; Rogers, 1994). Anomalies in the thickness of the mixed layer due to compression of isotherms around seamounts, Taylor columns, and eddies that are generated downstream of seamounts are thought to increase nutrient supply above and around seamounts and aid in the retention of particles and planktonic organisms (Boehlert and Mundy, 1993; Mullineaux and Mills, 1997; Mohn and Beckmann, 2002). This retention could then lead to an increase in secondary productivity over seamounts by entraining both food particles and the zooplankton over the seamount. However, evidence of enhanced primary productivity over a seamount that lasts long enough to influence higher trophic levels via bottom-up forcing is sparse and highly debated (Genin, 2004; Genin and Dower, 2007).

The abundance of many top marine predators, many of which feed on mesopelagic micronekton, have also been shown to be influenced by seamounts (Parin and Prut'ko,

1985; Wilson and Kaufmann, 1987; Rogers, 1994; Parin et al., 1997; Fock et al., 2002; Musyl et al., 2003). Fock et al. (2002) found that four dominant benthic predators found over Great Meteor Seamount, *Macroramphosus* spp., *Capros aper*, *Antigonia capros*, and *Zenopsis conchifer*, had diets consisting largely of pelagic plankton and micronekton and that these predators were feeding primarily on the margins of the summit where they were more likely to encounter and catch their prey which undergo diel vertical migration. In addition, Parin and Prut'ko (1985) found elevated catches of various sharks, skates, tunas, billfishes, and gempylids above Equator Seamount in the western tropical Indian Ocean, all with stomach contents consisting largely of a species myctophid fish.

Despite evidence of potentially increased food supply and increased foraging on mesopelagic micronekton over seamounts, as an entire group, they have been poorly sampled over and around seamounts. Many seamounts have summit elevations well within the depth ranges of the mesopelagic realm (approximately 300–1000 m below the sea surface) leading to possible interactions between these organisms and the seamount. A few studies have found evidence that the mesopelagic micronekton community is different over seamounts in comparison to the open-ocean habitat. In particular, there are certain species that may be defined as seamount-associated meaning that they occur exclusively, or in higher abundance, over a seamount as opposed to adjacent waters. Seamount-associated species have been described at several seamounts such as Southeast Hancock Seamount in the Pacific Ocean, Equator Seamount in the Indian Ocean and Bear Seamount in the Atlantic Ocean (Parin and Prut'ko, 1985; Boehlert and Genin, 1987; Moore et al., 2003).

Seamounts can also either attract or repel mesopelagic micronekton. If there is an aggregation or absence of mesopelagic micronekton over a seamount, it would not only be due to potential passive drifting in the current but also to active behavior. Behavioral reasons for aggregating in the vicinity of seamounts could be for reproduction or attraction to an increased food supply over and around seamounts (Wilson and Boehlert, 2004). Conversely, the mesopelagic micronekton community could be reduced or show no increase in abundance over the summit of a seamount because of increased predation or active avoidance of the shallow topography (Parin and Prut'ko, 1985; Pusch et al., 2004). As such, mesopelagic micronekton may aggregate around the flanks of the seamount, particularly while at depth during the day, instead of over the summit of the seamount.

South of the Big Island of Hawaii there is a rich tuna fishing ground located above Cross Seamount. The reason for this aggregation of tuna, mostly juvenile bigeye tuna (*Thunnus obesus*) and yellowfin tuna (*Thunnus albacares*), is unclear though one hypothesis is that there is increased foraging potential at the seamount as opposed to the open ocean (Holland et al., 1999). Bigeye tuna caught over Cross Seamount typically had fuller stomachs containing a greater diversity of prey items, and more mesopelagic prey items, than individuals that were caught away from the seamount (Grubbs et al., 2002). Yellowfin tuna also

feed on mesopelagic micronekton but to a lesser extent than bigeye (Grubbs et al., 2002).

While there is previous knowledge of the increased abundance of large pelagic predators and their diet at Cross Seamount, there is no previous knowledge of the mesopelagic micronekton community over and around the seamount. Evidence from tuna diet analysis suggests that there is an increased abundance of mesopelagic micronekton; however, no efforts have been previously made to directly test this hypothesis. Cross Seamount has a summit with an area of approximately 5.5 km² that rises to a flat plateau that has a minimum depth of 330 m below the sea surface. Additionally, Cross is located within a chain of seamounts with the closest neighbors being Washington Seamount approximately 20 km to the northeast and Swordfish Seamount approximately 35 km to the south-southeast. This structure may provide a large enough area to impact and change the community of mesopelagic micronekton. Preliminary analysis of acoustic surveys has shown dense aggregations of mesopelagic micronekton, or possibly other organisms, directly over the summit during the night and near the flanks of the seamount during the day (Reka Domokos, unpublished data). Therefore, in this study samples were collected by trawling over and near Cross Seamount to determine the influence of Cross Seamount on mesopelagic micronekton and ask three main questions: (1) is the abundance and/or biomass of organisms different over the summit of the seamount as opposed to away; (2) is the diversity or taxonomic composition of the assemblage different over the summit as opposed to away; and lastly (3) are there unique species located directly over the summit?

2. Methods

2.1. Sampling

Samples were collected from two cruises during late April of 2005 and late April and early May of 2007 aboard the NOAA research vessel *Oscar Elton Sette* (Fig. 1). Sampling during both years was conducted when there was no eddy activity in the region surrounding Cross Seamount (as determined by sea-surface temperature and height) and during the full moon. A dual warp modified Cobb trawl with an open mouth area of approximately 140 m² with a mesh size of 152 mm stretched at the mouth to a cod end lined with 3.2-mm knotless nylon delta mesh netting was used for collection. In an attempt to reduce damage to specimens during the trawl, the cod end of the net was modified for the 2007 cruise. A 1-m diameter, 5-m long plankton net with a mesh size of 1 mm was added to the end of the original cod end. At the end of the plankton net, a cod end bag constructed from plasticized canvas with dimensions of 30 cm diameter × 61 cm length was attached.

Two main types of trawls were conducted, day-deep and night-shallow, all of which were fished into the prevailing currents. Day-deep trawls were fished between 400 and 650 m during the day and night-shallow trawls were fished obliquely from 0 to 200 m during the night.

These depths were based on concurrently conducted acoustic surveys, which indicated the depths with the greatest density of sound scattering organisms. To determine and record the depths fished a Northstar Electronics Netmind Trawl Monitoring System was used. The Netminds were attached to the headrope and the wings of the trawl and sent to the ship via sonar data on latitude, longitude, temperature, and depth. Unfortunately, the Netmind did not always report data or the ship did not receive the data and also at times the data from the Netmind was incorrect. In 2007 a small time-depth recorder (TDR) was attached to the net in addition to the Netminds in order to make sure that depth data was recorded. The TDR recorded time, depth, and temperature information which could later be downloaded to a computer. Each trawl was fished at depth for 60 min at an average speed of 3 knots. This resulted in an approximate maximum possibility of 8.03×10^5 m³ of water filtered per trawl. All organisms from each trawl were preserved on board the ship with 10% formalin buffered with Borax. In the lab, all organisms from each trawl were sorted to the lowest possible taxonomic level. For each taxonomic level, counts were made of individuals and a weight was taken of the group as a whole.

The trawls conducted at Cross Seamount are divided into three main sample groups: summit, flank, and away. Summit trawls are defined as those trawls conducted directly over the flat plateau of the summit and in waters no deeper than 500 m. Away trawls are those trawls conducted within 14 km of the summit and in waters deeper than 1500 m. Flank trawls are trawls conducted on the slopes immediately surrounding the summit and in waters between 500 and 1500 m depths.

2.2. Analysis

Not all taxa which were captured and sorted from each trawl were used in the analysis portion of the study. Juveniles and some taxa smaller than 1 cm were excluded from the analysis based on the micronekton size criteria (between 2 and 20 cm) and inadequate quantitative sampling of organisms smaller than 1 cm. Certain juvenile organisms were included in the analysis because their size was larger than 1.5 cm. These were juvenile fishes, stomatopod larvae, and eel leptocephalus larvae. While juvenile fishes and stomatopod larvae are considered epipelagic, they are important in tuna diet and thus included in the analysis for comparative reasons. A few nektonic organisms that were larger than 30 cm were excluded based on their ability to effectively evade the large net. All gelatinous organisms, such as salps and scyphomedusa, were removed from the analysis because of inadequate sampling and frequent inability to identify the organisms after fixation. Additionally, while most organisms were sorted to the lowest taxonomic unit possible, some organisms, such as the myctophid fishes of the genus *Lampanyctus* sp. and most genera of crustaceans, were only reported in the analysis at the generic or familial level because of frequent trawl damage to the specimens which led to a frequent inability to identify

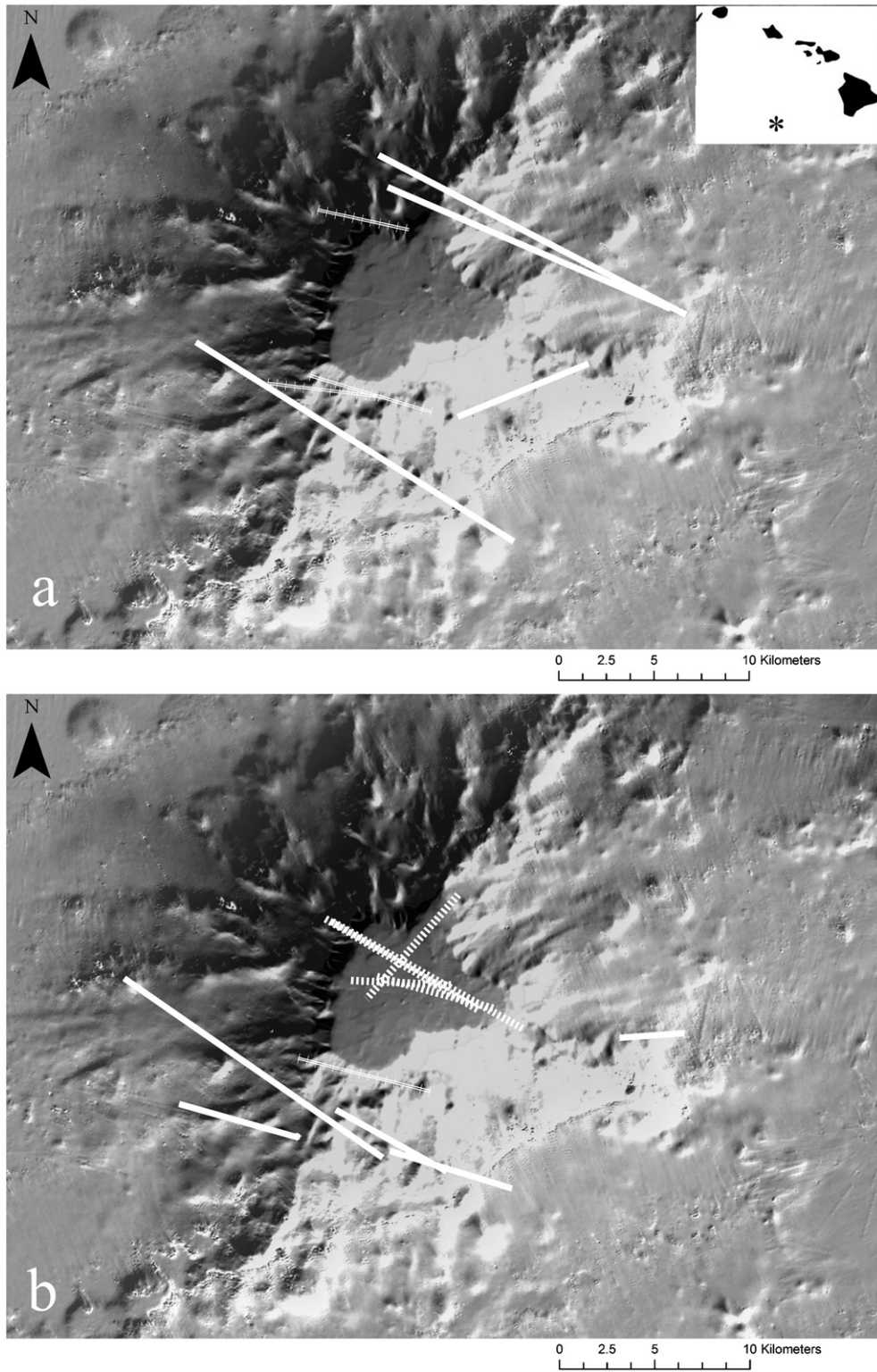


Fig. 1. Locations of the 18 trawls conducted over and around Cross Seamount: (a) day-deep trawls and (b) night-shallow trawls. Solid lines are away from summit trawls, dashed lines are flank trawls, and lines with perpendicular dash marks are summit trawls. There is variation within the trawl paths which reflect the start of operations to the end of operations (not just the distance fished at depth) and as such there is variation in the distance traveled. The inset in (a) shows the approximate location of Cross Seamount (depicted as an asterisk) relative to the Main Hawaiian Islands.

many specimens to the species level. A list of some of the species that could be identified from these genera or families are as follows: *Lampanyctus nobilis*, *Lampanyctus niger*, *Lampanyctus tenuiformis*, *Lampanyctus steinbecki*, *Lampanyctus festivus*, *Sergestes armatus*, *Sergestes vigilax*, *Sergestes consobrinus*, *Sergestes orientalis*, *Sergia bigemmus*, *Sergia inequalis*, *Sergia gardineri*, *Acanthephyra smithi*, and *Systellaspis debilis*. The species *Oplophorus gracilirostris* is listed in this study as *Oplophorus gracilirostris*?. This was because of slight variations in certain physical characteristics within the individuals caught.

Abundance and biomass, calculated as the count or weight of individuals per trawl, were compared using Mann–Whitney *U*-tests (Statistica 7.1). These comparisons were made at the specific, generic or familial level between the different trawl sample groups (i.e. night-shallow away vs. night-shallow summit). Initial comparisons were made between the 2005 and 2007 trawls of similar sample groups (i.e. between 2005 night-shallow away and 2007 night-shallow away) to determine if all trawls from similar sample groups could be pooled together. Next, comparisons were made between night-shallow summit (NSS) and night-shallow away (NSA), day-deep away (DDA) and NSA, and between day-deep flank (DDF) and DDA. All tests were reported as significant at a p -level ≤ 0.05 . While differences, in particular between DDA and NSA trawls, could be attributable to an organisms ability to avoid the net, particularly during the day. As such no identification of diel migrating or non-migrating taxa are made based on the comparisons between NSA and DDA trawls.

The trawl groups were also compared to one another using diversity indices. These indices were species richness, diversity, and evenness. The Margalef index of species richness, d , was calculated using the following equation:

$$d = \frac{(S - 1)}{\log(N)}$$

where S is the number of species and N is the total number of individuals. Species diversity was evaluated using Shannon's diversity index, H' , with the following equation:

$$H' = - \sum_{i=1}^S (P_i * \ln(P_i))$$

where S is the number of species and P_i is the proportion of S made up of the i th species. Lastly, evenness was calculated by using Pielou's evenness index, J' , with the following equation:

$$J' = \frac{H'}{\log(S)}$$

where H' is the Shannon's diversity index calculated with the previously mentioned equation and S is the number of species.

Rarefaction curves were generated to further investigate the difference in taxonomic diversity between trawl groups. This method estimated the number of different taxa that would be expected in a random sample of individuals taken from a larger sample group (James and

Rathburn, 1981). These estimations were then fit into a curve that depicts the increase in estimated taxa with increasing individuals until the total number of individuals and taxa present in the sample is reached. This would allow for a better comparison between large and small samples since taxonomic richness generally increases with increasing sample size (Hulpert, 1971). For instance, the estimated taxonomic diversity of all samples could be compared to one another at a given number of individuals for which all samples have at least that many individuals.

Finally, to investigate the relatedness of the communities sampled in each trawl group, a cluster analysis and similarity percentage procedure (SIMPER) were performed using Primer E-5 software (Clarke and Warwick, 2001). All abundance data used in the following analyses and procedures were square-root transformed because of their non-normal distribution and the large number of zeros (absences) in the data. A square-root transformation of the data was used to reduce the weight of the few taxa with large numbers of individuals (Clarke and Green, 1988). A Bray–Curtis similarity matrix was computed using the transformed abundance data for all taxa sorted from each trawl. This matrix was then used to construct a cluster analysis using group average linking. Main cluster groups were defined by the cluster analysis using ANOSIM ($p \leq 0.05$). The defined cluster groups were then used in the similarity percentage procedure (SIMPER) analysis. SIMPER was used to determine more precisely which taxa contributed to the overall similarity, or dissimilarity, between and within cluster groups.

3. Results

This study resulted in 18 total trawl samples. There are 2 NSS, 3 NSA, and 3 DDA in 2005 and 3 NSS, 2NSA, 1 DDA, 1 NSF, and 3 DDF in 2007. Locations for each of the trawls are depicted in Fig. 1. No day-deep trawls were conducted directly over the summit of Cross Seamount because of the shallow topography. For all taxonomic categories used in the analyses there were no significant differences between the NSS trawls from 2005 and 2007 or the DDA trawls from 2005 and 2007. Between the 2005 and 2007 NSA trawls there was one taxon that was significantly different ($p \leq 0.05$). This taxon was *Myctophum obtusirostrum*. This group is relatively rare with very low abundances in the trawls and thus does not contribute considerably to overall community structure.

3.1. Abundance and biomass

3.1.1. Away from the seamount

A comparison of the NSA and DDA trawls was necessary in order to describe the community of mesopelagic micronekton away from the summit of Cross Seamount and to allow for a brief comparison of this region to other studies that have described the assemblage of mesopelagic micronekton around the Hawaiian Islands. When all organisms are compared together, the NSA trawls have a higher total abundance of individuals

Table 1
Diversity indices for the trawl groups used in statistics

	NSS ($n = 5$)		NSA ($n = 5$)		DDA ($n = 4$)	DDF ($n = 3$)
S	30.40 ± 1.82	<	50.20 ± 6.53	>	30.50 ± 9.98	41.00 ± 16.09
N	279.60 ± 61.21	<	1021.00 ± 273.15	>	416.75 ± 122.80	435.67 ± 212.89
d	5.25 ± 0.52	<	7.14 ± 1.03	>	4.87 ± 1.43	6.58 ± 2.21
J'	0.75 ± 0.06	>	0.74 ± 0.02	>	0.63 ± 0.07	0.68 ± 0.07
H'	2.57 ± 0.21	<	2.89 ± 0.13	>	2.10 ± 0.27	2.47 ± 0.28

The diversity indices are as follows: S = number of species/taxa, N = number of individuals, d = Margalef index of species richness, J' = Pielou's evenness index, and H' = Shannon's diversity index. Significance is denoted by < or >, and is significant in the direction as indicated by the inequality sign (significance is at the $p \leq 0.05$, Mann-Whitney U -test).

than the DDA trawls ($p \leq 0.05$, Table 1). The cephalopods (Table 2), *Ctenopteryx* sp., *Abraliopsis pacifica* (Enoploteuthidae), Onychoteuthidae, and *Pterygioteuthis giardi* (Pyroteuthidae) all had higher abundances in the NSA trawls ($p \leq 0.05$). For crustaceans (Table 3), *Sergestes* sp. (Sergestidae), Hyperiidea amphipods, and stomatopod larvae were all higher in abundance in the NSA trawls ($p \leq 0.05$). There were nine myctophid fishes that were significantly higher in abundance in the NSA sample group than the DDA sample group ($p \leq 0.05$, Table 4). These species/genera are: *Benthosema suborbitale*, *Bolinichthys longipes*, *Ceratoscopelus warmingii*, *Diaphus fragilis*, *Diaphus schmidti*, *Hygophum proximum*, *Lampanyctus* sp., *Symbolophorus evermanni*, and *Triphoturus nigrescens* (Table 4). Juvenile fishes, eel leptocephalus larvae and *Vinciguerria* sp. (Phosichthyidae) also showed a higher abundance in the NSA trawls than the DDA trawls ($p \leq 0.05$, Table 4). In contrast to the majority of the results, four stomiiform fishes were higher in abundance in the DDA trawls than the NSA trawls ($p \leq 0.05$). These taxa were: *Cyclothone* sp. (Gonostomatidae), *Gonostoma atlanticum* (Gonostomatidae), *Danophos oculatus* (Sternoptychidae), and *Argyropelecus* sp. (Sternoptychidae) (Table 4).

Most all the patterns in abundance between the NSA and DDA trawls were paralleled by biomass, though there was a small difference. All the cephalopod, myctophid, and stomiiform groups that were different in abundance were also different in biomass between the two trawl depths, with the trends previously described in the abundance comparison holding true for each of the groups (Tables 2–4). Of the crustaceans, Hyperiidea amphipods and *Sergestes* sp. do not have higher biomass in the NSA trawls despite being higher in abundance. It appears that these two groups have larger individuals in the DDA trawls. For the Hyperiidea amphipods this can be explained by the presence of *Cystosoma* sp., a genus of larger individuals, which were found in some of the DDA trawls but not in the NSA trawls. The eel leptocephalus larvae also did not have higher biomass in the NSA trawls despite having a higher abundance, again implying that larger individuals are residing at depth.

3.1.2. Seamount summit and away

Overall, there are fewer organisms over the summit of Cross Seamount than away, with the summit having approximately 2/3 fewer individuals ($p \leq 0.05$, Table 1). In the cephalopod category (Table 2), the family Pyroteuthi-

dae as a whole and the genus *Ctenopteryx* sp. were both higher in abundance in the NSA trawls than the summit trawls ($p \leq 0.05$). In contrast, the cranchiid squid *Liocranchia reinhardti* was higher in abundance in the NSS trawls than the NSA trawls ($p \leq 0.05$). Of the crustacean category (Table 3), only one taxon, *Sergestes* sp. (Sergestidae), was found to be higher in abundance in the NSA trawls than the NSS trawls ($p \leq 0.05$). Nine species of myctophid fishes were significantly more abundant in the NSA sample group, with five of these species completely absent in the NSS sample group ($p \leq 0.05$, Table 4). *Bolinichthys longipes*, *Ceratoscopelus warmingii*, *Diaphus schmidti*, and *Symbolophorus evermanni* all occurred in both the NSA and NSS sample groups with a higher abundance away from the summit ($p \leq 0.05$). *Diaphus fragilis*, *Diaphus rolfbolini*, *Lampadena urophaos*, *Lampanyctus* sp., and *Triphoturus nigrescens* are all quite abundant in the NSA sample group but completely absent from the NSS sample group. The only stomiiform group that was found to be different between the night-shallow two trawl groups was *Vinciguerria* sp. with a higher abundance in the NSA sample group ($p \leq 0.05$, Table 4).

All of the taxonomic groups that were different between the NSS and NSA trawls based on abundance data were also found to be different based on biomass data. However, six additional taxonomic groups had higher biomass in the NSA trawls than the NSS trawls without being higher in abundance (Tables 2–4). The family Cranchiidae, as a whole, and four species of myctophid fishes had higher biomass in the NSA trawls than the NSS trawls ($p \leq 0.05$). The three species of myctophid fishes were *Benthosema suborbitale*, *Diaphus mollis*, and *Hygophum proximum*.

3.2. Community composition

Of all the trawl groups, the NSA trawls had the highest species diversity (H') and abundance of organisms ($p \leq 0.05$, Table 1). However, this may be due to the fact that the other trawls (DDA, DDF, and NSS) had lower numbers of total individuals (N) than the NSA trawls. On average, the NSS trawls had 60% fewer individuals and 40% fewer taxa (S) than the NSA trawls (Table 1). Despite these differences in number of individuals and species diversity, the NSS and NSA trawl groups both had a relatively even distribution of individuals amongst taxa present as indicated by a Pielou's evenness index (J') close to one (Table 1). The DDF and DDA trawl groups both had

Table 2
Cephalopod abundance (average number per trawl ± standard deviation) and biomass (in parentheses following abundance, average grams per trawl ± standard deviation)

	NSS (n = 5)		NSA (n = 5)		DDA (n = 4)	DDF (n = 3)	NSF (n = 1)
Cranchiidae	10.20 ± 9.44(1.85 ± 1.42)	(<)	12.40 ± 7.70(11.03 ± 4.84)	>(>)	1.50 ± 1.73(0.52 ± 0.66)	0.67 ± 1.15(0.92 ± 1.59)	7(7.31)
<i>Helicocranchia beebei?</i>	–		2.40 ± 3.58(3.08 ± 4.22)		–	–	5(5.01)
<i>Helicocranchia pfefferi</i>	–		–		0.25 ± 0.50(0.04 ± 0.08)	0.33 ± 0.58(0.69 ± 1.20)	–
<i>Leachia pacifica</i>	–		1.80 ± 4.02(0.38 ± 0.84)		–	–	–
<i>Liocranchia reinhardti</i>	9.60 ± 8.73(1.69 ± 1.47)	>(>)	0.20 ± 0.45(0.07 ± 0.15)		–	–	2(1.70)
<i>Liocranchia valdiviae</i>	0.20 ± 0.45(0.14 ± 0.31)		2.80 ± 4.66(0.38 ± 0.55)		–	–	–
<i>Megalocranchia fisheri</i>	–		3.80 ± 6.50(3.71 ± 6.10)		–	–	–
<i>Sandalops melancholicus</i>	–		0.80 ± 1.79(3.24 ± 7.24)		0.50 ± 0.58(0.40 ± 0.70)	–	–
<i>Taonius pavo</i>	–		0.60 ± 1.34(0.19 ± 0.42)		–	–	1(0.60)
Enoploteuthidae	5.40 ± 3.78(14.91 ± 21.27)		31.60 ± 35.05(33.53 ± 45.92)	>	1.50 ± 0.58(2.80 ± 2.23)	0.33 ± 0.58(0.68 ± 1.18)	10(31.63)
<i>Abrialiopsis</i> sp. A	0.80 ± 0.84(0.85 ± 1.55)		11.20 ± 15.22(12.38 ± 20.64)		0.50 ± 1.00(0.36 ± 0.71)	–	6(4.53)
<i>Abrialiopsis</i> sp. C	0.20 ± 0.45(0.07 ± 0.15)		3.40 ± 4.22(2.17 ± 2.89)		–	–	–
<i>Abrialiopsis pacifica</i>	2.20 ± 3.03(2.33 ± 4.19)		11.60 ± 14.06(12.74 ± 20.21)	>	0.25 ± 0.50(0.10 ± 0.19)	–	1(2.50)
<i>Abrialia trigonura</i>	1.40 ± 1.52(2.62 ± 3.91)		4.80 ± 4.55(5.73 ± 6.04)		0.75 ± 0.96(2.35 ± 2.71)	0.33 ± 0.58(0.68 ± 1.18)	1(0.26)
<i>Enoploteuthis higginsii</i>	–		0.20 ± 0.45(0.35 ± 0.77)		–	–	–
<i>Enoploteuthis reticulata</i>	0.40 ± 0.55(8.98 ± 19.88)		0.20 ± 0.45(0.07 ± 0.16)		–	–	2(24.34)
Pyroteuthidae	2.40 ± 1.34(1.04 ± 0.69)	<(<)	10.60 ± 5.94(5.52 ± 2.22)	>(>)	–	0.33 ± 0.58(2.41 ± 4.17)	2(0.98)
<i>Pterygioteuthis giardi</i>	1.60 ± 0.89(0.68 ± 0.59)		7.40 ± 5.08(3.25 ± 2.76)	>(>)	–	–	2(0.98)
<i>Pterygioteuthis microlampas</i>	0.40 ± 0.55(0.19 ± 0.28)		2.20 ± 4.38(0.48 ± 0.86)		–	–	–
<i>Pyroteuthis addolux</i>	0.20 ± 0.45(0.12 ± 0.28)		1.00 ± 1.41(1.79 ± 2.70)		–	0.33 ± 0.58(2.41 ± 4.17)	–
Chtenopterygidae	–	<(<)	1.80 ± 1.48(2.93 ± 2.66)	>(>)	–	–	–
Onychoteuthidae	3.00 ± 6.71(0.84 ± 1.88)		5.20 ± 4.44(7.15 ± 8.70)	>(>)	–	–	9(6.08)

Data for families are an average of all species within the family in addition to individuals only identified to the family level. Significance is denoted by > or < (abundance followed by biomass in parentheses), and is significant in the direction as indicated by the inequality sign (significant at $p \leq 0.05$; Mann-Whitney *U*-test).

Table 3
Crustacean abundance (average number per trawl ± standard deviation) and biomass (in parentheses following abundance, average grams per trawl ± standard deviation)

	NSS (n = 5)		NSA (n = 5)		DDA (n = 4)		DDF (n = 3)		NSF (n = 1)
Oplophoridae	25.80 ± 26.47 (9.85 ± 10.06)		33.80 ± 21.94 (13.32 ± 11.88)		44.25 ± 48.68 (12.46 ± 7.00)		19.33 ± 9.02 (24.02 ± 25.25)		26 (6.36)
<i>Oplophorus gracilirostris</i>	2.40 ± 5.37 (2.04 ± 4.56)		8.20 ± 9.73 (8.66 ± 9.96)		29.75 ± 31.29 (10.26 ± 4.49)		6.00 ± 5.57 (12.11 ± 11.74)		4 (0.55)
<i>Janicella spinacauda</i>	23.40 ± 26.88 (7.81 ± 9.75)		23.00 ± 19.66 (3.44 ± 2.39)		13.25 ± 19.17 (2.06 ± 2.71)		6.33 ± 5.69 (2.19 ± 2.00)		22 (5.81)
<i>Systallapsis</i> sp.	–		1.20 ± 2.68 (0.73 ± 1.64)		0.75 ± 1.50 (2.06 ± 2.71)		3.67 ± 5.51 (2.62 ± 4.49)		–
<i>Acanthephyra</i> sp.	–		0.40 ± 0.55 (0.43 ± 0.63)		0.50 ± 1.00 (0.10 ± 0.20)		3.00 ± 2.64 (6.96 ± 11.52)		–
Pandalidae	–		3.80 ± 4.02 (0.82 ± 0.98)		6.75 ± 10.44 (1.57 ± 2.67)		0.33 ± 0.58 (0.11 ± 0.19)		–
Sergestidae	6.40 ± 5.03 (0.27 ± 0.13)	< (<)	53.40 ± 26.21 (7.63 ± 7.64)	>	12.00 ± 9.63 (2.19 ± 2.89)		11.33 ± 9.45 (4.47 ± 5.78)		2 (4.15)
<i>Sergia</i> sp.	0.20 ± 0.45 (0.02 ± 0.05)		10.80 ± 13.54 (5.52 ± 7.21)		0.25 ± 0.50 (0.07 ± 0.14)		–		2 (4.15)
<i>Sergestes</i> sp.	6.20 ± 5.22 (0.25 ± 0.12)	< (<)	42.60 ± 20.24 (2.11 ± 0.64)	>	11.75 ± 9.29 (2.12 ± 2.76)		11.33 ± 9.45 (4.47 ± 5.78)		–
Benthosymidae									
<i>Gennadas</i> sp.	–		3.80 ± 5.22 (0.63 ± 0.87)		–		0.33 ± 0.58 (0.13 ± 0.21)		–
Lophogastridae									
<i>Lophogaster</i> sp.	1.20 ± 0.84 (0.04 ± 0.04)		1.20 ± 1.64 (0.04 ± 0.06)		1.75 ± 2.22 (0.06 ± 0.08)		–		2 (0.03)
Hyperiid amphipod	9.00 ± 7.81 (0.36 ± 0.25)		8.60 ± 3.13 (0.56 ± 0.38)	>	3.50 ± 1.73 (0.28 ± 0.22)	(<)	4.67 ± 4.04 (4.33 ± 3.07)		15 (1.24)
Stomatopod	55.00 ± 41.35 (4.58 ± 5.59)		77.60 ± 81.24 (9.29 ± 8.37)		–		–		6 (2.02)

Data for families are an average of all species within the family in addition to individuals only identified to the family level. Significance is denoted by > or < (abundance followed by biomass in parentheses), and is significant in the direction as indicated by the inequality sign (significant at p ≤ 0.05; Mann-Whitney U-test).

Table 4

Fishes abundance (average number per trawl ± standard deviation) and biomass (in parentheses following abundance, average grams per trawl ± standard deviation)

	NSS (n = 5)		NSA (n = 5)		DDA (n = 4)		DDF (n = 3)		NSF (n = 1)
Myctophidae	55.40 ± 18.74 (25.23 ± 9.74)	< (<)	547.40 ± 99.72 (405.01 ± 82.70)		55.00 ± 41.41 (50.09 ± 49.86)		117.67 ± 93.77 (107.22 ± 85.54)		725 (634.93)
<i>Diogenichthys atlanticus</i>	–		0.60 ± 0.89 (0.05 ± 0.08)		–		–		–
<i>Benthoosema fibulatum</i>	15.60 ± 18.42 (8.59 ± 12.07)		–		0.25 ± 0.50 (0.02 ± 0.05)		0.33 ± 0.58 (0.51 ± 0.88)		–
<i>Benthoosema suborbitale</i>	0.20 ± 0.45 (0.03 ± 0.07)	(<)	1.60 ± 1.52 (0.51 ± 0.57)	> (>)	–		–		–
<i>Bolinichthys distofax</i>	–		–		6.75 ± 8.06 (10.00 ± 13.11)		2.67 ± 2.52 (7.28 ± 6.71)		–
<i>Bolinichthys longipes</i>	0.20 ± 0.45 (0.02 ± 0.05)	< (<)	25.20 ± 16.81 (14.82 ± 9.63)	> (>)	1.75 ± 2.87 (0.17 ± 0.31)		5.00 ± 8.66 (3.17 ± 5.48)		53 (27.83)
<i>Ceratoscopelus warmingii</i>	10.20 ± 14.50 (2.89 ± 3.58)	< (<)	104.40 ± 72.09 (77.60 ± 48.29)	> (>)	0.25 ± 0.50 (0.02 ± 0.03)		10 ± 16.46 (3.13 ± 5.37)		128 (168.76)
<i>Diaphus anderseni</i>	0.20 ± 0.45 (0.15 ± 0.33)		1.20 ± 1.79 (1.21 ± 1.81)		0.25 ± 0.50 (0.38 ± 0.76)		–		7 (5.10)
<i>Diaphus bertelseni</i>	0.20 ± 0.45 (0.31 ± 0.69)		–		–		–		–
<i>Diaphus brachycephalus</i>	0.60 ± 0.89 (0.13 ± 0.17)		10.80 ± 10.76 (3.06 ± 2.85)		0.25 ± 0.50 (0.06 ± 0.12)		0.33 ± 0.58 (0.10 ± 0.18)		1 (0.68)
<i>Diaphus fragilis</i>	–	< (<)	14.60 ± 12.03 (44.44 ± 31.40)	> (>)	–		1.67 ± 2.08 (3.39 ± 4.30)		12 (54.47)
<i>Diaphus metapoclampus</i>	–		–		0.50 ± 0.58 (1.98 ± 2.28)		0.33 ± 0.58 (0.70 ± 1.21)		–
<i>Diaphus mollis</i>	2.00 ± 1.58 (0.44 ± 0.56)	(<)	15.20 ± 19.04 (5.32 ± 7.25)		10.50 ± 8.70 (9.69 ± 7.23)		7.00 ± 10.39 (17.47 ± 28.36)		4 (1.26)
<i>Diaphus perspicillatus</i>	0.20 ± 0.45 (0.13 ± 0.30)		3.40 ± 5.50 (4.49 ± 7.17)		0.75 ± 0.96 (0.92 ± 1.25)		1.67 ± 2.89 (1.59 ± 2.75)		9 (6.74)
<i>Diaphus phillipsi</i>	–		–		0.50 ± 1.00 (1.12 ± 2.24)		–		–
<i>Diaphus rolfbolini</i>	–	< (<)	4.00 ± 3.08 (7.75 ± 6.70)		0.50 ± 1.00 (2.23 ± 4.46)		1.67 ± 1.53 (2.03 ± 3.05)		3 (1.18)
<i>Diaphus schmidti</i>	10.60 ± 10.16 (5.03 ± 4.71)	< (<)	163.20 ± 125.67 (89.22 ± 78.75)	> (>)	11.00 ± 13.34 (5.73 ± 7.39)		16.67 ± 22.30 (10.12 ± 14.47)		162 (86.10)
<i>Diaphus trachops</i>	1.00 ± 1.73 (2.22 ± 4.74)		1.00 ± 2.24 (1.88 ± 4.20)		5.50 ± 6.19 (13.93 ± 16.56)		7.00 ± 5.57 (17.82 ± 14.19)		–
<i>Hygophum proximum</i>	4.60 ± 2.88 (2.21 ± 2.35)	(<)	46.00 ± 32.77 (27.15 ± 20.71)	> (>)	4.50 ± 5.45 (1.78 ± 2.37)	(<)	33.67 ± 24.83 (28.89 ± 25.27)		41 (30.07)
<i>Hygophum reinhardti</i>	0.20 ± 0.45 (0.07 ± 0.15)		1.00 ± 1.22 (0.50 ± 1.00)		–		–		–
<i>Lampadena luminosa</i>	–		0.20 ± 0.45 (0.31 ± 0.70)		–		0.33 ± 0.58 (0.86 ± 1.49)		–
<i>Lampadena urophaos</i>	–	< (<)	4.40 ± 5.50 (6.32 ± 6.14)		0.50 ± 1.00 (0.03 ± 0.05)		3.67 ± 4.72 (0.38 ± 0.54)		11 (1.99)
<i>Lamppanyctus sp.</i>	–	< (<)	81.60 ± 67.24 (78.08 ± 55.73)	> (>)	–	(<)	6.33 ± 9.24 (4.19 ± 6.69)		234 (211.49)
<i>Lobianchia gemellarii</i>	–		0.60 ± 0.89 (0.78 ± 1.31)		0.50 ± 0.58 (0.74 ± 0.93)		0.33 ± 0.58 (0.25 ± 0.44)		–
<i>Myctophum brachgnathos</i>	–	(<)	0.67 ± 1.63 (0.19 ± 0.46)	> (>)	–		–		–
<i>Myctophum lychnobium</i>	–		0.17 ± 0.41 (0.04 ± 0.11)		–		–		1 (5.90)
<i>Myctophum nitidulum</i>	–		0.17 ± 0.41 (0.52 ± 1.26)		–		–		–
<i>Myctophum obtusirostrum</i>	0.40 ± 0.89 (0.64 ± 1.44)		0.83 ± 0.98 (1.37 ± 1.92)		–		–		–
<i>Myctophum selnoides</i>	–		0.17 ± 0.41 (0.06 ± 0.16)		0.20 ± 0.45 (0.36 ± 0.77)		0.33 ± 0.58 (0.33 ± 0.56)		1 (2.11)
<i>Myctophum spinosum</i>	–		–		–		0.67 ± 0.58 (0.37 ± 0.58)		–
<i>Symbolophorus evermanni</i>	0.60 ± 0.89 (1.61 ± 2.83)	< (<)	10.40 ± 5.32 (24.71 ± 21.05)	> (>)	–		0.33 ± 0.58 (0.05 ± 0.08)		17 (24.57)
<i>Triphoturus nigrescens</i>	–	< (<)	14.40 ± 16.46 (2.64 ± 3.02)	> (>)	1.25 ± 2.50 (0.14 ± 0.28)		0.33 ± 0.58 (0.05 ± 0.09)		–
Gonostom atidae	9.20 ± 7.56 (0.61 ± 0.42)	< (<)	63.40 ± 22.60 (14.45 ± 11.54)	<	209.75 ± 89.50 (28.65 ± 29.68)		196.33 ± 100.30 (141.08 ± 193.04)		3 (1.12)
<i>Gonostoma atlanticum</i>	–		–	< (<)	2.00 ± 1.83 (1.27 ± 0.91)		3.33 ± 3.51 (1.91 ± 2.01)		–
<i>Sigmops ebelingi</i>	–		1.00 ± 1.41 (0.10 ± 0.16)		10.00 ± 16.06 (16.82 ± 26.79)		47.33 ± 59.10 (120.88 ± 175.99)		2 (0.14)
<i>Sigmops gracile</i>	–		–		–		1.00 ± 1.00 (1.94 ± 2.78)		–
<i>Cyclothone sp.</i>	1.20 ± 1.64 (0.03 ± 0.06)		4.20 ± 9.39 (0.14 ± 0.32)	< (<)	182.00 ± 92.88 (7.30 ± 4.72)		139.33 ± 109.79 (6.88 ± 3.44)		–
<i>Diplophos sp.</i>	–		0.40 ± 0.55 (0.64 ± 1.40)		0.50 ± 1.00 (0.92 ± 1.83)		0.67 ± 1.15 (2.87 ± 4.96)		1 (0.98)
Phosichthyidae									
<i>Vinciguerria sp.</i>	7.60 ± 7.89 (0.42 ± 0.42)	< (<)	56.00 ± 21.06 (7.52 ± 3.52)	> (>)	13.00 ± 16.75 (1.76 ± 1.82)	> (>)	1.00 ± 1.00 (0.14 ± 0.14)		39 (6.21)
Melanostom iidae	–		1.00 ± 2.24 (1.37 ± 3.06)		–		0.33 ± 0.58 (0.30 ± 0.52)		–
<i>Eustomias sp.</i>	–		0.80 ± 1.79 (2.11 ± 4.71)		–		–		1 (0.22)

<i>Bathophilus</i> sp.	–	–		0.25 ± 0.50 (0.67 ± 1.34)	0.33 ± 0.58 (1.96 ± 3.39)	
Malacosteidae	–	0.20 ± 0.45 (0.24 ± 0.55)		–	1.33 ± 2.31 (13.07 ± 22.54)	–
Idiacanthidae	–	2.20 ± 4.92 (8.35 ± 18.67)		–	–	–
Astronesthidae	–	1.00 ± 1.22 (2.72 ± 5.98)		–	–	1 (1.32)
Stomiidae	–	–		1.67 ± 0.58 (6.27 ± 5.75)	>(>)	–
Sternoptychidae						–
<i>Danaphos oculatus</i>	0.40 ± 0.55 0.16 ± 0.33	0.20 ± 0.45 (0.01 ± 0.03)	<(<)	5.75 ± 6.95 (0.85 ± 1.43)	5.33 ± 7.57 (0.96 ± 1.29)	–
<i>Argyropelecus</i> sp.	–	–	<(<)	7.75 ± 7.41 (12.06 ± 8.11)	5.67 ± 4.16 (9.31 ± 8.24)	–
<i>Sternoptyx</i> sp.	–	–		1.00 ± 1.41 (0.05 ± 0.07)	8.33 ± 12.74 (7.99 ± 13.41)	–
Eel leptocephalus larvae	10.60 ± 8.17 (3.44 ± 2.71)	32.25 ± 39.20 (6.08 ± 3.12)	>	1.50 ± 1.00 (3.01 ± 3.63)	1.33 ± 0.58 (5.16 ± 8.50)	31 (7.86)
Juvenile Fish	156.40 ± 153.80 (10.41 ± 7.07)	52.5 ± 18.64 (14.36 ± 9.07)	>(>)	–	–	130 (18.22)
“Other Mesopelagic Fish”	3.80 ± 4.97 (1.75 ± 3.47)	12.00 ± 8.83 (6.18 ± 5.03)		10.50 ± 11.70 (9.06 ± 10.13)	(<)	40.67 ± 32.33 (5.16 ± 8.50)

Data for families are an average of all species within the family in addition to individuals only identified to the family level. Significance is denoted by > or < (abundance followed by biomass in parentheses) and is significant in the direction as indicated by the inequality sign (significant at $p \leq 0.05$; Mann–Whitney U -test).

evenness indices (J') that are similar and lower than the night-shallow trawl groups, indicating a less even distribution of individuals amongst the taxa present in these two groups.

The use of rarefaction curves allowed for a better comparison between trawl groups that have different numbers of individuals or sample sizes. When each of the trawl groups were compared to one another at a potential sample size of only 979 individuals (the total number of individuals sampled from the smallest trawl group, NSF) the DDF trawl group had the highest number of estimated taxa of all the trawl groups at 62 estimated taxa (Fig. 2). The NSA trawl group, which had the highest species diversity when total number of individuals sampled (4659 total individuals) was taken into account, had slightly fewer estimated taxa at this smaller potential sample size. This implies that while the DDF group had a lower species diversity index (H') than the NSA group, this may be a result of this group having a lower number of total individuals sampled.

The NSA and NSS trawls separated into distinct clusters (40% similarity) based on the Bray–Curtis similarity matrix constructed using the transformed abundance data from the lowest possible taxonomic units sorted from each trawl (Fig. 3; ANOSIM: $R = 0.99$; $p \leq 0.05$). The DDA trawls separated into two clusters that have significantly different assemblages of organisms (Fig. 3; ANOSIM: $R = 0.691$; $p \leq 0.05$). The two cluster groups were named day-deep away shallow (DDAS) and day-deep away deep (DDAD). These day-deep trawls were significantly separated from the night-shallow trawls at approximately the 27% similarity level (ANOSIM: $R = 0.95$; $p \leq 0.05$). The flank trawls did not separate into distinct clusters from the other trawl away types. The one

NSF trawl was grouped within the NSA trawls and the three DDF trawls within the DDA trawls, indicating that the taxonomic composition of these trawls were not very dissimilar from that of the away trawls and as such were included in these cluster groups for the SIMPER analysis. The NSA cluster was compared to the two DDA cluster groups, and the NSS and NSA cluster groups were compared using the SIMPER analysis. No direct comparison was made between NSS and the two DDA cluster groups because of their difference in location and water depth.

The DDA trawls were divided into two cluster groups DDAS and DDAD. DDAS trawls were fished at an average depth between 481 and 539 m and the DDAD trawls were fished on average between 518 and 560 m. The DDAS trawls had an average of 61.66% overall similarity and DDAD trawls had an average of 50.48% overall similarity. In both groups the highest contributor to similarity within the individual groups was *Cyclothone* sp., accounting for 34.87% of the overall similarity for DDAS and 24.34% of the overall similarity for DDAD. The taxon that contributed the most to the overall dissimilarity between DDAS and DDAD (contributing 6.99% to the overall dissimilarity) was the caridean shrimp *Oplophorus gracilirostris*?. This species was found to be higher in abundance in the DDAS trawls, with an average of 51.5 individuals per trawl. The DDAD trawls had an average of only 4.40 individuals per trawl. The DDAD trawls were more diverse than the DDAS trawls with 22 taxa contributing to 90% of the overall similarity within the DDAD cluster and only 10 taxa contributing to 90% of the overall similarity within the DDAS cluster.

The NSA cluster group had an average similarity of 61.82% and was the most diverse cluster group, with 25

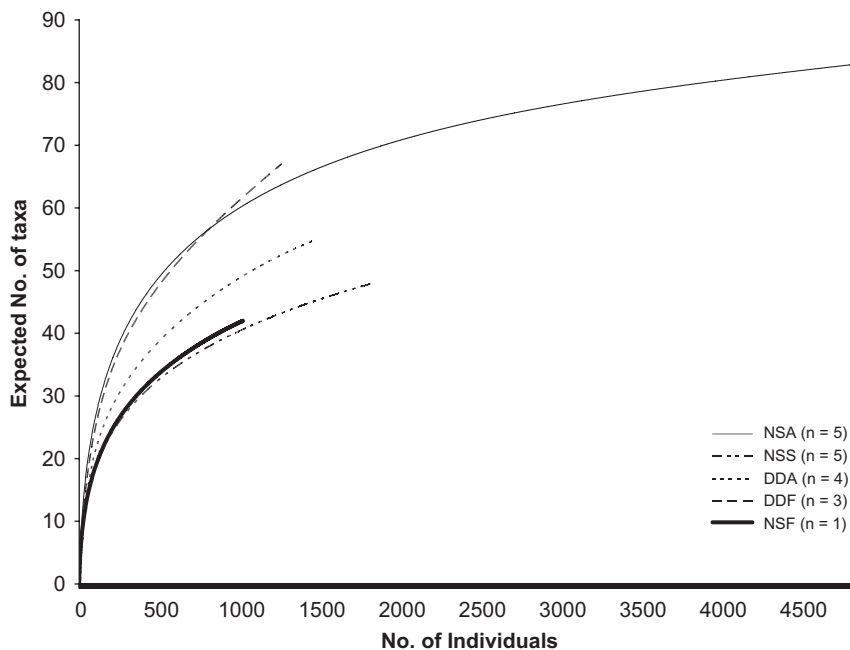


Fig. 2. Rarefaction curves for the five different trawl groups. The individual trawls within each trawl group were summed to create the curve for each group.

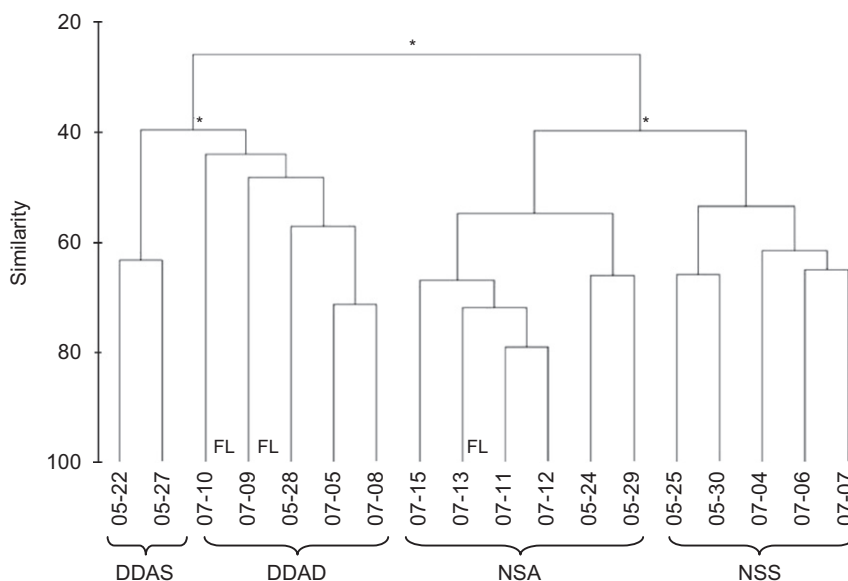


Fig. 3. Cluster analysis constructed using the Bray-Curtis similarity matrix with square root transformation of the abundance data. Similarity is reported as percentages. The trawl names are coded as xx-yy (i.e. 05-22), with xx referring to the last two digits of the year the trawl was conducted and yy referring to the trawl number from that year. Asterisks denote that the node reflects a significant difference in the assemblage of organisms between two cluster groups (ANOSIM $p \leq 0.05$). FL to the upper-right of some trawl names denotes that these are flank trawls.

taxonomic groups contributing to 90% of the overall similarity within the cluster group. The myctophid *Diaphus schmidti*, with an average of 163 individuals per trawl, accounted for the majority of the similarity between the trawls (10.59%). The top 90% of the overall similarity contains 12 myctophids, one gonostomatid, eel leptocephalus larvae, four crustaceans, stomatopod larvae, and five cephalopods (Fig. 4). The taxonomic composition of the NSA community was numerically dominated by myctophid fishes, followed by crustaceans and then cephalopods (Fig. 5b). When the epipelagic juvenile categories were eliminated from the analysis there was little change to the overall taxonomic composition (Fig. 5d). While the 2005 and 2007 trawls separated into two different groups, the groups had an average of 54.70% similarity to one another and the taxonomic composition of the assemblages were not significantly different (ANOSIM: $R = 1.00$, $p > 0.05$).

The NSS cluster group had an overall average similarity of 57.46%, with the highest contributor to the overall similarity being juvenile fishes at 20.56% of the overall similarity. Juvenile fishes were also the most abundant group within the NSS cluster, with an average abundance of 156.40 individuals per trawl. A total of 15 taxonomic groups contributed to the top 90% of the overall similarity within the NSS cluster group. These groups were five myctophids, one gonostomatid, three crustaceans, two cephalopods, juvenile fishes, stomatopod larvae, and eel leptocephalus larvae (Fig. 4). The taxonomic composition of the NSS community was numerically dominated by epipelagic juvenile fishes followed closely by stomatopod larvae, and then mesopelagic fishes, crustaceans, and cephalopods (Fig. 5a). When the epipelagic juvenile categories were excluded the composition of the community changed dramatically and was dominated by meso-

pelagic fishes (mostly myctophids) followed closely by crustaceans and finally cephalopods (Fig. 5c). The 2005 and 2007 trawls separated into two different groups, however both groups had an average of 53.44% similarity to one another and the taxonomic composition of the assemblages were not significantly different (ANOSIM: $R = 0.92$, $p > 0.05$).

The NSA cluster group had an overall average similarity of 20.07% to the DDAS cluster group and an overall average of 27.15% to the DDAD cluster group. The five taxa that accounted for the majority of the differences between the NSA cluster and both the DDAS and DDAD clusters were *Diaphus schmidti* (7.59% dissimilarity to DDAS; 5.11% dissimilarity to DDAD), *Cyclothone* sp. (6.18% dissimilarity to DDAS; 7.13% dissimilarity to DDAD), *Ceratoscopelus warmingii* (6.36% dissimilarity to DDAS; 5.11% dissimilarity to DDAD), *Lampanyctus* sp. (5.94% dissimilarity to DDAS; 4.92% dissimilarity to DDAD), and juvenile fish (5.21% dissimilarity to DDAS; 4.84% dissimilarity to DDAD). Of these five taxa only *Cyclothone* sp. was more abundant in both the DDAD and DDAS trawls while the other four were higher in abundance in the NSA trawls.

The overall average similarity between the NSA and NSS cluster groups was 39.66%. *Lampanyctus* sp. was the largest contributor to the difference at 7.23% of the dissimilarity followed next by *Diaphus schmidti* (7.01% dissimilarity) and *Ceratoscopelus warmingii* (5.71% dissimilarity). These top three contributors were all myctophids and were in much higher abundance in the NSA trawls than in the NSS trawls with *Lampanyctus* sp. completely absent from NSS trawls. Fourteen taxonomic groups contributed to 50% of the dissimilarity, of which three occurred in higher abundance in the NSS trawls while the other 11 occurred in higher abundance in the NSA trawls. The three that were higher in abundance in the NSS trawls

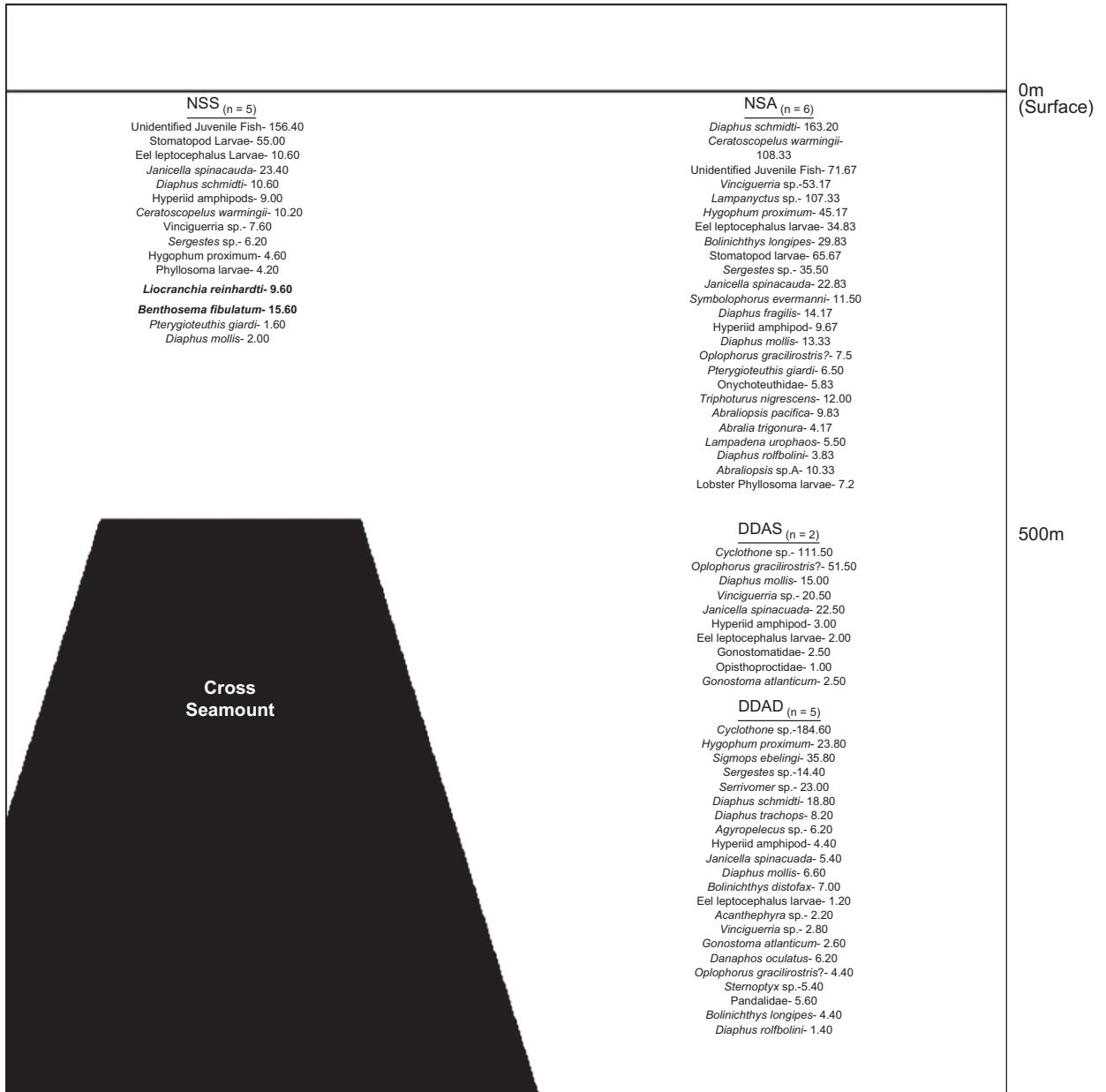


Fig. 4. A schematic of Cross Seamount listing the taxa that contribute to 90% of the overall similarity within the four cluster groups as determined by the SIMPER analysis. The numbers next to the taxa are the average abundances (ind./trawl) within the cluster. The two taxa in bold under the NSS column are the two possible seamount-associated species at Cross Seamount.

were juvenile fishes, *Benthosema fibulatum* and *Janicella spinacauda*.

3.3. Flanks

Over the flanks of the seamount, only one night-shallow trawl was conducted. This prevented robust statistical comparisons of biomass and abundance to other night-shallow trawls, but a few qualitative comparisons could be made. There appeared to be a large abundance of fishes and a lower abundance of crustaceans

in the NSF trawl when compared to the NSA and NSS trawl groups (Fig. 6). The large abundance of fishes, mostly myctophids, would appear to make the NSF trawl similar to the NSA trawl group; however, the low abundances of crustaceans and cephalopods are more characteristic of the NSS trawl group (Fig. 6). The NSF trawl had no *Sergestes* sp., very little *Sergia* sp. and a markedly lower abundance of stomatopod larvae and Hyperiid amphipods (Table 3). The cephalopod families Enoplateuthidae and Onychoteuthidae were also very low in abundance in comparison to the night-shallow away trawls (Table 2).

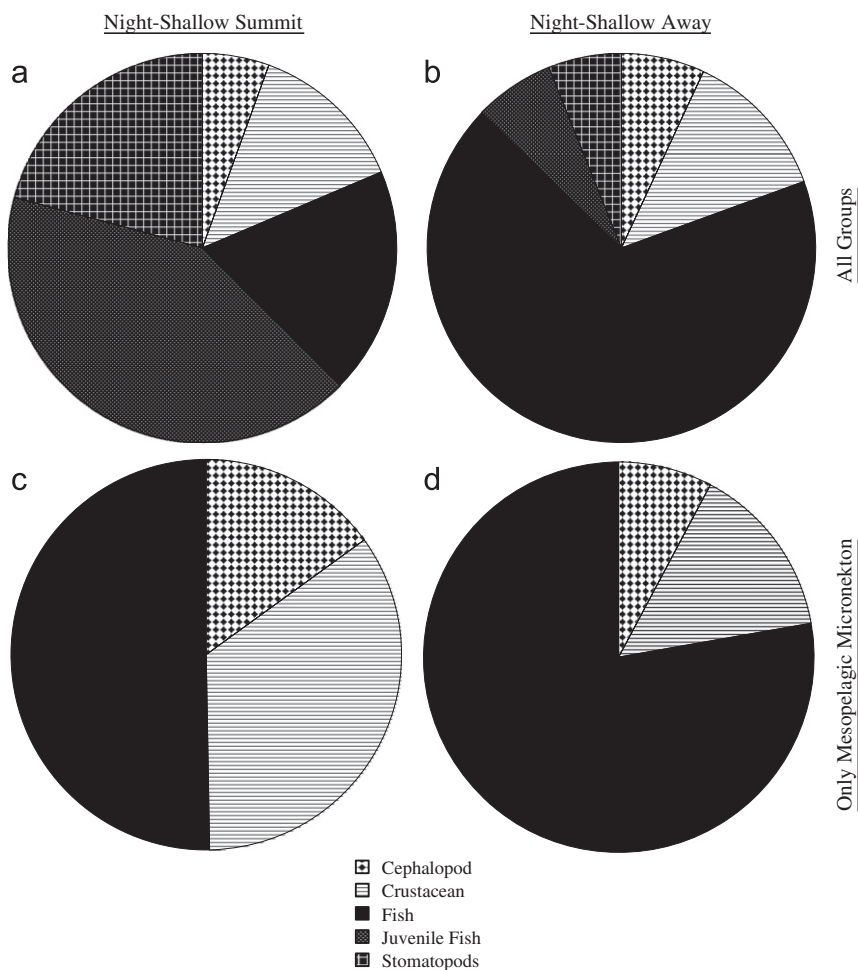


Fig. 5. The taxonomic composition of the night-shallow summit (a and c) and night-shallow away (b and d) communities based on the abundance of broad taxonomic groups. a–b includes the epipelagic juvenile groups of juvenile fish and stomatopod larvae in addition to the mesopelagic categories. c–d includes only mesopelagic micronekton groups.

Statistical analyses could be conducted on the DDF sample group ($n = 3$) for comparison with the DDA sample group. Both trawl groups had relatively the same number of species (S) and number of individuals (N) (Table 1). The DDF trawl group had an average number of 435.67 individuals and the DDA trawl group had an average number of 416.75 individuals. When the abundance and biomass of taxa were analyzed between the two trawl groups few differences were found. This corroborated the cluster analysis which showed the DDF trawls intermixed within the cluster of the DDA trawls. Several taxa were found to have higher biomass in the DDF group without having a higher abundance, implying that perhaps the individuals caught in the DDF group were larger. These taxa include hyperiid amphipods, *Hygophum proximum*, *Lampanyctus* sp., and other fishes (Tables 3 and 4). The “other fishes” category of the DDF group consisted largely of paralepidids, which were quite large in size and absent from the DDA group, and serrivomer eels, which are large in size and more abundant in the DDF group. In the DDA group, the “other fishes” category consisted of a

higher abundance of a gempylid fish species, *Nealotus tripes*, of which the individuals were relatively small in size. The family Stomiidae is the only taxon that has both a higher abundance and higher biomass in the DDF trawl group. Lastly, one genus, *Vinciguerria* sp., was found to have both a higher abundance and a higher biomass in the DDA trawl group (Table 4).

4. Discussion

This study has resulted in a description of the local assemblage of mesopelagic micronekton over and around Cross Seamount. This assemblage does appear to differ greatly with previous studies from the region around Hawaii despite the locality and the use of a very large Cobb trawl. Previous descriptions of the mesopelagic micronekton communities in the open ocean around Hawaii by Maynard et al. (1975) and Reid et al. (1991) have both used Isaacs–Kidd midwater trawls (IKMT) which had 3 and 2 m wide square mouths, respectively.

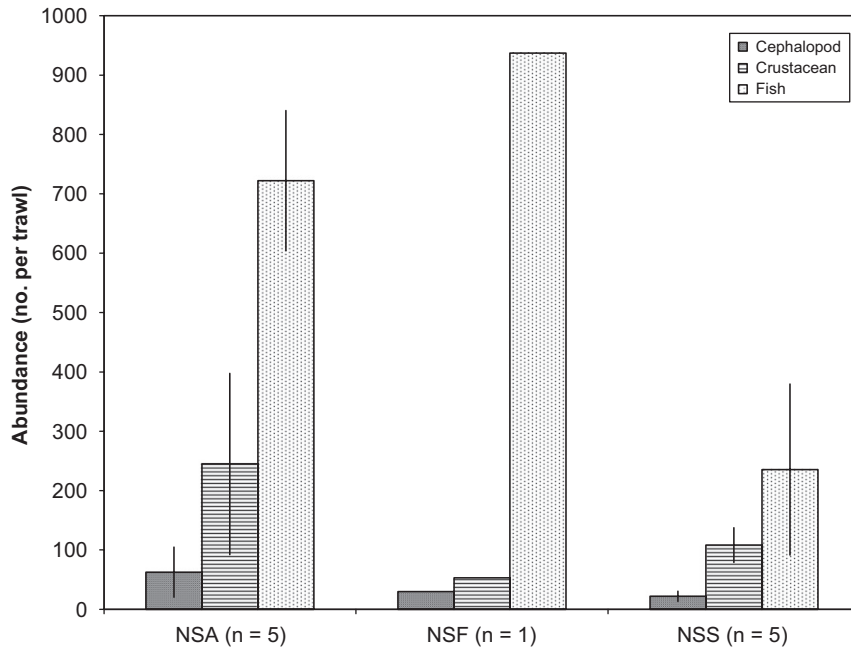


Fig. 6. Bar graph depicting the average abundances of cephalopods, crustaceans and fish with standard deviation for the NSA and NSS trawl groups.

In addition to the IKMT, Reid et al. (1991) used a large Cobb trawl with an approximate 200 m² mouth opening, but collected fewer samples with this larger net. Studies at other seamounts have all used nets quite a bit smaller than the one used in this study, ranging from small 2 m wide IKMT to a Young Fish Trawl with an 80 m² mouth opening (Boehlert and Seki, 1984; Pusch et al., 2004; Wilson and Boehlert, 2004). The advantage to using a larger net is that many of the mesopelagic micronekton species, such as most squids and larger myctophids, are known to successfully avoid smaller nets (Clarke, 1983; Reid et al., 1991). These organisms are the main diet of many benthic and pelagic predators and thus are important to this study. In this study the net had a very large mouth opening (approximately 140 m²) and large mesh size, which allowed for a faster towing speed, both of which would help to reduce the ability of these organisms to avoid the net. Unfortunately, these characteristics reduced the ability of the net to adequately sample small and delicate organisms. However, the addition of the modified cod end in 2007 did result in a greater catch of juvenile and smaller organisms, though these organisms were still excluded from the analysis to remain consistent with the 2005 samples. Lastly, large nets with non-rectangular mouth openings, such as the net used in this study, can result in an inability to precisely calculate the volume of water filtered for each trawl and prevents the use of calculations to estimate the number or biomass of organisms per area of ocean (Kashkin and Parin, 1983; McClatchie et al., 2000).

Despite the differences in the nets used in previous studies, the structure of mesopelagic micronekton assemblage described away from the seamount in this study is comparable to that found in past studies in the region and

can be considered representative of the open-ocean community. This is important because of the relatively close proximity of the trawls conducted off the seamount summit to the summit itself (Fig. 1). Maynard et al. (1975) described the night-shallow micronekton community as dominated numerically by penaeidean shrimps followed by myctophid fishes, euphausiids, caridean shrimps, and gonostomatid fishes. The main structure of the night-shallow community away from the seamount summit is very similar and is dominated largely by myctophids followed by crustaceans (mainly caridean shrimps and stomatopod larvae), *Vinciguerria* sp. and then squids. Euphausiids were not reported in this study because of inadequate sampling. Reid et al. (1991) also had a description of the night-shallow community surrounding the Main Hawaiian Islands and reported this community as numerically dominated by fishes (mostly myctophid fishes), followed by shrimps (mostly Sergestid shrimps) and very few cephalopods. The day-deep community described in this paper is also very similar to that found by Maynard et al. (1975), with *Cyclothone* sp. by far dominating the community in abundance followed by a myctophid species (*Diaphus mollis*), several shrimps and other gonostomatid species. A comparison can be made of the myctophid community away from the seamount summit to a past study near the Main Hawaiian Islands. Clarke (1983) used a combination of 2- and 3-m IKMT and a large modified Cobb trawl to sample the myctophid community. The most abundant species from this past study were, in decreasing order *Ceratoscopelus warmingii*, *Lampanyctus steinbecki*, *Triphoturus nigrescens*, and *Lampanyctus niger* (Clarke, 1983). In the present study, the top four most abundant myctophid species away from the seamount summit were *Diaphus schmidti*, *Ceratoscopelus*

warmingii, *Lampanyctus* sp., and *Hygophum proximum*. The slight difference in the most abundant myctophid species from this present study to the Clarke (1983) study could be due to the fact only a large Cobb trawl was used instead of three different nets of different sizes.

4.1. Is the abundance or biomass different over the summit?

Directly over the summit of Cross Seamount the average abundance and biomass of organisms is drastically less than away from the summit. This is in contrast to the data collected from concurrent acoustic surveys by Domokos (unpublished data) and will be further explored in a future paper. The overall abundance of organisms in the NSS community is approximately one-third of the abundance of the NSA community, largely as a result of the absence or reduced abundance of certain taxa (Tables 2–4). Pusch et al. (2004) in their study of Atlantis and Great Meteor Seamount in the Atlantic Ocean found similar results in which the abundance of mesopelagic fishes above the seamount was considerably less than in adjacent waters. Haury et al. (2000) also found similar results regarding the zooplankton community at seamounts in the North Pacific. A reason for this reduction in overall abundance may be increased predation of mesopelagic micronekton over the summit. As migrating micronekton descend to their daytime depths, those that were located above the summit of the seamount will come into close proximity to the summit or flanks before reaching their normal daytime depths. This could compact the organisms and make them readily available to both benthic and pelagic predators by preventing the organisms from descending to depths where they can effectively hide from predators. Many seamounts have increased abundance of both pelagic and benthic predators (Parin and Prut'ko, 1985; Holland et al., 1999; Sibert et al., 2000; Fock et al., 2002). At Cross Seamount, not only is there a high abundance of tunas over the summit, but diet analysis of bigeye and yellowfin tuna caught over the summit showed that these individuals had fuller stomachs containing large amounts of mesopelagic shrimps, fishes, and squids than individuals caught in the open ocean (Grubbs et al., 2002). The taxa that bigeye consume heavily over the summit are Oplophorid shrimps, followed by Sergestid shrimps, Myctophid fishes, and cephalopods (Grubbs et al., 2002). All of these taxa, except for the Oplophorid shrimps, showed decreased abundance over the summit as opposed to away from the summit (Tables 2–4). This evidence supports predation as a possible cause for the decrease in abundance over the summit for most taxa except for the oplophorid shrimps.

In addition to predation decreasing the number of individuals over the summit, the mesopelagic micronekton may also be actively avoiding or changing their migration behavior over the summit of the seamount. Most mesopelagic micronekton tend to avoid coming close to either the seafloor or sea surface, areas where they cannot hide and escape from predators as effectively, though some have been shown to aggregate over banks and other shallow topography (Benoit-Bird and Au, 2004;

Genin, 2004; Gartner et al., 2008). Additionally, instead of being located over the summit, many of the organisms may instead be found in high abundance over the flanks of the seamount at all times or perhaps only during the daytime. Results from trawls conducted by Pusch et al. (2004) over the slopes of Great Meteor and Atlantis Seamounts indicated that there was a decrease in density of organisms and number of species over the slopes as opposed to the open ocean; however, this decrease was not as large as that found over the summit of both seamounts. Boehlert and Genin (1987) and Parin and Prut'ko (1985) both found high concentrations of mesopelagic organisms along the seamount flanks during the day and a more diffuse scattering of organisms above the flank and summit during the night as indicated by acoustic transects. Horizontal migrations have been documented in mesopelagic micronekton around the main Hawaiian Islands in which the organisms resided at depths greater than 400 m during the day and migrated horizontally and vertically to shallow, near-shore waters off the islands (Benoit-Bird and Au, 2004). This could also potentially happen around seamounts. Organisms may migrate horizontally and vertically to the shallower waters over the summit but migrate back to deeper waters over the flanks for the daytime in order to avoid the shallow topography and predation. However, there is little evidence to suggest that this occurs at Cross Seamount. There is a low abundance of organisms over the summit at night, which does not indicate that organisms are migrating to be over the summit at night from the flanks. In addition the flanks of Cross Seamount were sampled, though not adequately enough to indicate if there is a large community of mesopelagic micronekton residing along the flanks. The day-deep flank trawls do not appear very different from the day-deep away trawls with regards to abundance of organisms and taxonomic composition of the community. The one night-shallow flank trawl suggests a very high abundance of fishes (Fig. 6); however, this was a result from only one trawl sampled. Additional sampling and analysis of the flanks would result in a better description and understanding of the impact of Cross Seamount on the mesopelagic micronekton community. In addition, analysis of acoustic transects over the flanks and summit of the seamount, with particular emphasis during times of maximum migration in the evening and pre-dawn, would aid in describing where the majority of the organisms are during different parts of the day and potentially their migration patterns.

4.2. Is the diversity or taxonomic composition of the community different over the summit?

The composition of the community over the summit of the seamount is quite different than the community away from the summit. Results from the cluster analysis (Fig. 3), show that all of the trawls conducted over the summit of Cross Seamount cluster into a distinct group from the trawls conducted away from the summit. The diversity indices indicate that the species diversity is lower over the

summit. Even though there are fewer total numbers of individuals sampled over the summit, the rarefaction curve shows the summit community also has fewer numbers of taxa per any given number of individuals than away from summit community (Fig. 2). A look at the taxonomic composition of the mesopelagic micronekton community over the summit reveals that while fishes, in particular Myctophid fishes, numerically dominate the community, crustaceans are also quite abundant and numerically contribute to a larger portion of the overall taxonomic composition of the community than away from the summit (Figs. 5c and d). However, when the epipelagic juveniles are included in the taxonomic composition of the community, the summit of the seamount is dominated numerically by juvenile fishes and stomatopod larvae while away from the seamount there appears to be little change in the taxonomic composition with the addition of the epipelagic juveniles (Figs. 5a and b). This may imply that over the summit of the seamount the dramatic decrease in abundance and biomass of organisms may largely be due to a large decrease in mesopelagic micronekton but not epipelagic micronekton. It may be either avoidance of the summit or higher rates of predation on mesopelagic micronekton rather than epipelagic micronekton may be the cause.

Interestingly, all of the mesopelagic micronekton taxa that are absent over the summit have daytime depths that are greater than the summit depth (>500 m), while the taxa that are lower in abundance over the summit have daytime depths that are approximately equal to the depth of the summit. This evidence supports that mesopelagic micronekton are avoiding the summit of Cross Seamount. The myctophid genus *Lampanyctus*, which is completely absent over the summit (Table 4), has average daytime depths between 590 and 1200 m, well below the depth of the summit (Clarke, 1983). This is also true for many shrimps. *Gennadas* sp., *Acantheephyra* sp., and *Systellaspis* sp. are completely absent over the summit, and all have daytime depths greater than 500 m (Table 3; Omori, 1974). In contrast, those vertically migrating taxa that are still present over the summit of the seamount, but in reduced abundance compared to away trawls, have daytime depth ranges that range from above to slightly below the depth of the summit. Many cephalopods, such as *Pterygioteuthis giardi* and *Abraliopsis* sp., have daytime depths between 300 and 600 m (Roper and Young, 1975). Other taxa that follow this trend are the myctophid fish *Diaphus schmidtii*, with daytime depths between 490 and 625 m (Clarke, 1983), and the shrimps *Sergestes* sp. and *Sergia* sp., with daytime depths between 200 and 700 m (Omori, 1974).

Despite the many differences in abundance of certain taxa, the summit community does not appear to differ greatly from the community away from the summit regarding size of organisms. In this study the size of organisms is estimated by comparing the biomass recorded for each taxa. In the few taxa that did appear to differ in size, they all appeared to have larger sizes away from the summit of the seamount than over the summit. The family Cranchiidae, as a whole, appears to have larger individuals away from the summit. This is mainly due to the fact that a number of the larger species of cranchiid

squids are absent in summit trawls. One species in particular, *Helicocranchia beebei*, is one of the larger species in the family and is completely absent over the summit (Table 2). In the family Myctophidae, four species were found to have larger individuals off the summit as opposed to on. These three are *Benthosema suborbitale*, *Diaphus mollis*, and *Hygophum proximum*. There was, however, large variation in the catch of these four myctophids leading to large standard deviations in the abundance and biomass averages. The apparent absence of some larger individuals over the summit again supports the explanation that many mesopelagic micronekton are avoiding the summit of the seamount. Many larger individuals tend to reside at deeper depths during the day than smaller individuals in order to more effectively hide from visual predators (Clarke, 1983; Hays et al., 1994). The summit would prevent these individuals from reaching these deep depths, making them more vulnerable to predation.

4.3. Are there unique species over the summit?

Over the summit there appears to be two possible seamount-associated species. The cranchiid squid *Liocranchia reinhardti* was found to be significantly higher in abundance over the summit than away (Table 2). This species, however, does not appear to be exclusive to the summit as one was caught in a trawl away from the summit. The other species is the myctophid fish *Benthosema fibulatum*. While this species was not statistically more abundant over the summit because of highly variable catch rates, none were caught away from the summit (Table 4). Reid et al. (1991) describe both species as part of the Hawaiian mesopelagic boundary community, which is defined as species that are associated with the flanks of the main Hawaiian Islands. The other species listed by Reid et al. (1991) as being of the boundary-layer community were not found to be significantly higher in abundance over the summit. Of the other species listed as belonging to the Hawaiian boundary community, five were not caught in any of the trawls in this present study and three were caught in relatively low abundances both over and away from the summit. The three that were caught in low abundance in comparison to the Reid et al. (1991) study both over and away from the summit were *Diaphus trachops*, *Oplophorus gracilirostris*, and *Abralia trigonura*. The summit of Cross Seamount is in the 400–700 m depth range, which is listed in Reid et al. (1991) as being the daytime depth of the boundary layer, yet these species were not higher in abundance over the summit. One possible explanation could be that many near-shore communities often show increased concentrations of primary and secondary (zooplankton) productivity and many mesopelagic micronekton are known to consume zooplankton (Maynard et al., 1975; Benoit-Bird and Au, 2004). Currently there is not much information regarding the primary and secondary productivity at Cross Seamount. Studies focusing on primary and secondary production are needed to further understand the dynamics of the mesopelagic micronekton community over

and around Cross Seamount. In particular, a determination of whether or not there is an increased forage base for the mesopelagic micronekton over, or perhaps immediately away from, the seamount would help to explain the distribution and composition of the mesopelagic micronekton community over and around Cross Seamount. Additionally, Cross Seamount may not actively retain larvae of possible seamount-associated organisms through circulation patterns and its relatively small size in comparison to the Main Hawaiian Islands. This may not encourage the recruitment of larvae of seamount- or island-associated organisms to Cross Seamount. Many seamounts, such as Southeast Hancock Seamount and Great Meteor Seamount, have not been found to actively retain larvae of seamount-associated species, and in fact the larvae of most organisms have been found to be lower in abundance over the seamount as opposed to away (Boehlert and Mundy, 1993).

5. Conclusion

Seamounts can provide a unique habitat for many species and can help describe the patchy distribution of many organisms throughout the world's oceans. Understanding the dynamics that lead to this patchiness will aid in better management, not only for these organisms but also for the commercially important species that prey on these organisms. Mesopelagic micronekton has an important role as prey for many marine predators and in the flux of organic matter to the deep sea. Cross Seamount is a site of increased tuna abundance relative to the adjacent open ocean. A proposed reason for this increased abundance is that there is an increased forage base over the seamount. This study has shown that Cross Seamount does have an impact on the abundance and community structure of the local mesopelagic micronekton community. Even though there is a large decrease in abundance of organisms over the summit when compared to the nearby away community, this decrease may be due to predation and/or to active avoidance of the seamount summit by deeper migrating taxa. Additionally, preliminary evidence indicates that the flanks may be of interest for future studies. While the cluster analysis did not separate the flank trawls from the away trawls, the rarefaction curve generated for the day-deep flank community indicates that despite having a low total number of individuals sampled there is high species diversity. Future work should focus more on the flanks of the seamount to better understand its influence on the mesopelagic micronekton community. While the summit is the site of high concentrations of pelagic predators, it may be the flanks that have the largest positive impact on their forage base, mesopelagic micronekton. Another area of future work is constructing a detailed description of the presence and distribution of phytoplankton and zooplankton over and around the summit along with a description of the physical flow patterns over and around the summit. There is strong evidence that Cross Seamount is influencing large marine predators and mesopelagic micronekton, but

the mechanisms behind this influence are unknown and cannot be fully determined without further studies.

Acknowledgments

This project was funded by Cooperative Agreement NA17RJ1230 between the Joint Institute for Marine and Atmospheric Research (JIMAR) and the National Oceanic and Atmospheric Administration (NOAA). The views expressed herein are those of the authors and do not necessarily reflect the views of NOAA of any of its subdivisions. L. De Forest would like to acknowledge and thank her Master's thesis committee; Jeffrey Drazen, Margaret McManus and John Sibert. We would like to thank our collaborators; Reka Domokos, Jeffrey Polovina, Michael Seki, and Richard Young, for their help with this project and the crew of the NOAA R/V *Oscar Elton Sette*. We are grateful for all the help and hard work of William Misa, Molly-Jean Martin, Katrina Loewy, and Krystle Turkington. Funding was provided by a grant from the Pelagic Fisheries Research Program (PFRP).

References

- Benoit-Bird, K.J., Au, W.W.L., 2004. Diel migration of an island-associated sound-scattering layer. *Deep-Sea Research I* 51, 707–719.
- Boehlert, G.W., Genin, A., 1987. A review of the effects of seamounts on biological processes. In: Keating, B.H., Fryer, P., Batiza, R., Boehlert, G.W. (Eds.), *Seamounts, Islands and Atolls*. Geophysical Monograph 43. American Geophysical Union, Washington, pp. 319–334.
- Boehlert, G.W., Mundy, B.C., 1993. Ichthyoplankton assemblages at seamounts and oceanic islands. *Bulletin of Marine Science* 53 (2), 336–361.
- Boehlert, G.W., Seki, M.P., 1984. Enhanced micronekton abundance over Mid-Pacific mountains. *EOS Transactions of the American Geophysical Union* 65, 928.
- Brodeur, R.D., Yamamura, O., 2005. *Micronekton of the North Pacific*. PICES Scientific Report No. 30, p. 1–115.
- Clarke, T.A., 1983. Comparison of abundance estimates of small fishes by three towed nets and preliminary results of the use of small purse seines as sampling devices. *Biological Oceanography* 2, 311–340.
- Clarke, K.R., Green, R.H., 1988. Statistical design and analysis for a "biological effects" study. *Marine Ecology Progress Series* 46, 213–226.
- Clarke, K.R., Warwick, R.M., 2001. Primer E (5) Computer Program. Natural Environmental Research Council, Plymouth.
- Fock, H.O., Matthiessen, B., Zidowitz, H., von Westernhagen, H., 2002. Diel and habitat-dependent resource utilization by deep-sea fishes at the Great Meteor seamount: niche overlap and support for the sound scattering layer interception hypothesis. *Marine Ecology Progress Series* 244, 219–233.
- Haurly, L., Fey, C., Newland, C., Genin, A., 2000. Zooplankton distribution around four eastern North Pacific seamounts. *Progress in Oceanography* 45, 69–105.
- Hays, C.G., Proct, C.A., John, A.W.G., Warner, A.J., 1994. Interspecific differences in the diel vertical migration of marine copepods: the implications of size, color and morphology. *Limnology and Oceanography* 39, 1621–1629.
- Hidaka, K., Kawaguchi, K., Murakami, M., Takahashi, M., 2001. Downward transport of organic carbon by diel migratory micronekton in the western equatorial Pacific: its quantitative and qualitative importance. *Deep-Sea Research I* 48, 1923–1939.
- Holland, K.N., Kleiber, P., Kajiura, S.M., 1999. Different residence times of yellowfin tuna, *Thunnus albacares*, and bigeye tuna, *T. obesus*, found in mixed aggregations over a seamount. *Fishery Bulletin* 97, 392–395.
- Hulpert, S.H., 1971. The nonconcept of species diversity: a critique and alternative parameters. *Ecology* 52 (4), 577–586.
- Gartner Jr., J.V., Sulak, K.J., Ross, S.W., Neccaise, A.M., 2008. Persistent near-bottom aggregations of mesopelagic animals along the North

- Carolina and Virginia continental slopes. *Marine Biology* 153, 825–841.
- Genin, A., 2004. Bio-physical coupling in the formation of zooplankton and fish aggregations over abrupt topographies. *Journal of Marine Systems* 50, 3–20.
- Genin, A., Dower, J.F., 2007. Seamount plankton dynamics. In: Pitcher, T.J., Morato, T., Hart, P.J.B., Clark, M.R., Haggan, N., Santos, R.S. (Eds.), *Seamounts: Ecology, Fisheries and Conservation*. Fish and Aquatic Resources Series 12. Blackwell Publishing, Iowa, pp. 85–100.
- Genin, A., Noble, M., Lonsdale, P.F., 1989. Tidal currents and anticyclonic motions on two North Pacific seamounts. *Deep-Sea Research* 36 (12), 1803–1815.
- Grubbs, R.D., Holland, K., Itano, D., 2002. Comparative trophic ecology of yellowfin and bigeye tuna associated with natural and man-made aggregation sites in Hawaiian waters. 15th Meeting of the Standing Committee on Tuna and Billfish, (SCTB 15) Working Paper, YFT-6.
- James, F.C., Rathburn, S., 1981. Rarefaction, relative abundance, and diversity of avian communities. *The Auk* 98, 785–800.
- Karpouzi, V.S., Watson, R., Pauly, D., 2007. Modelling and mapping resource overlap between seabirds and fisheries on a global scale: a preliminary assessment. *Marine Ecology Progress Series* 343, 87–99.
- Kashkin, N.I., Parin, N.V., 1983. Quantitative assessment of micronektonic fishes by non-closing gear (a review). *Biological Oceanography* 2, 263–287.
- Maynard, S.D., Riggs, F.V., Walters, J.F., 1975. Mesopelagic micronekton in Hawaiian waters: faunal composition, standing stock, and diel vertical migration. *Fishery Bulletin* 73 (4), 726–736.
- McClatchie, S., Thorne, R.E., Grimes, P., Hanchet, S., 2000. Ground truth and target identification for fisheries acoustics. *Fisheries Research* 47, 173–191.
- Mohn, C., Beckmann, A., 2002. The upper ocean circulation at Great Meteor Seamount. *Ocean Dynamics* 52, 179–193.
- Moore, J.A., Vecchione, M., Collette, B.B., Gibbons, R., Hartel, J.K., Galbraith, J.K., Turnispeed, M., Southworth, M., Watkins, E., 2003. Biodiversity of Bear Seamount, New England Seamount Chain: results of exploratory trawling. *Journal of Northwest Atlantic Fishery Science* 31, 363–372.
- Mullineaux, L.S., Mills, S.W., 1997. A test of the larval retention hypothesis in seamount-generated flows. *Deep-Sea Research I* 44 (5), 745–770.
- Musyl, M.K., Brill, R.W., Boggs, C.H., Curran, D.S., Kazama, T.K., Seki, M.P., 2003. Vertical movements of bigeye tuna (*Thunnus obesus*) associated with islands, buoys, and seamounts near the main Hawaiian Islands from archival tagging data. *Fisheries Oceanography* 12 (3), 152–169.
- Noble, M., Mullineaux, L.S., 1989. Internal tidal currents over the summit of Cross Seamount. *Deep-Sea Research* 36 (12), 791–1802.
- Omori, M., 1974. The biology of pelagic shrimps in the ocean. *Advances in Marine Biology* 12, 233–324.
- Parin, N.V., Prut'ko, V.G., 1985. The thalassial mesobenthopelagic ichthyocoene above the Equator Seamount in the western tropical Indian Ocean. *Oceanology* 25 (6), 781–783.
- Parin, N.V., Mironov, A.N., Nesis, K.N., 1997. Biology of the Nazca and Sala y Gómez Submarine Ridges, an outpost of the Indo-West Pacific fauna in the Eastern Pacific Ocean: composition and distribution of the fauna, its communities and its history. *Advances in Marine Biology* 32, 145–242.
- Pauly, D., Trites, A.W., Capuli, E., Christensen, V., 1998. Diet composition and the trophic levels of marine mammals. *ICES Journal of Marine Science* 55, 467–481.
- Porteiro, F.M., Sutton, 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*. Fish and Aquatic Resources Series 12. Blackwell Publishing, Iowa, pp. 101–116.
- Pusch, C., Beckmann, A., Porteiro, M., von Westernhagen, H., 2004. The influence of seamounts on mesopelagic fish communities. *Archives of Fishery and Marine Research* 51 (1–3), 165–186.
- 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. *Marine Biology* 109, 427–440.
- Rogers, A.D., 1994. The biology of seamounts. *Advances in Marine Biology* 30, 305–350.
- Roper, C.F.E., Young, R.E., 1975. Vertical distribution of pelagic cephalopods. *Smithsonian Contributions to Zoology* 209, 1–51.
- Sibert, J., Holland, K., Itano, D., 2000. Exchange rates of yellowfin and bigeye tunas and fishery interaction between Cross Seamount and near-shore FADs in Hawaii. *Aquatic Living Resources* 13, 225–232.
- Smith, D.K., Jordan, T.H., 1988. Seamount statistics in the Pacific Ocean. *Journal of Geophysical Research* 93 (B4), 2899–2918.
- Wilson, C.D., Boehlert, G.W., 2004. Interaction of ocean currents and resident micronekton at a seamount in the central North Pacific. *Journal of Marine Systems* 50, 39–60.
- Wilson, R.R., Kaufmann, R.S., 1987. Seamount biota and biogeography. In: Keating, B.H., Fryer, P., Batiza, R., and Boehlert, G.W. (Eds.), *Seamounts, Islands and Atolls*. Geophysical Monograph 43. American Geophysical Union, Washington, pp. 355–377.