



Micronekton abundance and biomass in Hawaiian waters as influenced by seamounts, eddies, and the moon

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ABSTRACT

Micronekton abundance, biomass, and community composition was determined from 58 Cobb trawl samples taken from 2005 to 2008 at several locations in the lee of the Hawaiian Islands. The results indicated a strong influence of the lunar illumination on micronekton abundance and biomass. This effect was evident in shallow night tows and probably was the result of lunar light affecting the nighttime depths of migrating species. The abundance and biomass of micronekton is remarkably consistent between years and areas in Hawaiian waters after the effects of moon phase are accounted for. Micronekton, principally migratory myctophids, were reduced over the summit of Cross Seamount but not Finch Seamount that has a summit below the daytime depth of most migrators. However, during a new moon, micronekton abundance over Cross seamount was similar to surrounding areas either because of altered migration patterns or because predators such as tunas cannot forage as effectively at night without lunar illumination. Species belonging to the Hawaiian mesopelagic boundary layer community were found to vary in presence and abundance between years at Cross Seamount suggesting that a consistent seamount associated fauna does not exist. Sparse sampling of a cyclonic mid-ocean eddy suggested very high micronekton abundance and biomass both in shallow waters at night but also at depth during the day. Although preliminary, these results suggest that eddies may aggregate the micronekton which probably feed on the enhanced secondary productivity.

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1. Introduction

Oceanic micronekton are a diverse assemblage of small (~2–20 cm) fishes, shrimps, and squids forming a key trophic link between top predators and zooplankton (Brodeur and Yamamura, 2005). Commercially important pelagic fishes – including albacore tuna, bigeye tuna, and swordfish – feed directly on micronekton, particularly mesopelagic micronekton (Bertrand et al., 2002; Choy et al., 2009; Dagorn et al., 2000; Markaida and Sosa-Nishizaki, 1998; Palko et al., 1981; Tsarin, 1997). Knowledge of the processes affecting micronekton distribution would be of great value in estimating the distribution and yield of large oceanic fish stocks affected by patterning of food supply.

The dynamic oceanic environment includes mesoscale oceanographic and bathymetric features that influence the micronekton community. In Hawaii, there is an important commercial fishery for large pelagic fishes and the catch of tunas and billfishes

is not evenly distributed—some locations have higher catch rates than others. For instance, Cross seamount located south of the island of Oahu, exhibits higher catch rates of bigeye tuna and it has been hypothesized that this is the result of concentrations of micronekton (Holland and Grubbs, 2007). In contrast, trawl studies at this seamount find reduced micronekton abundance and biomass, likely the result of the animals actively avoiding seamount summits shallower than their daytime depths (De Forest and Drazen, 2009). Studies of micronekton along island flanks and over seamount summits have often found a community of animals taxonomically distinct from the nearby open ocean, sometimes referred to as mesopelagic boundary layer communities (MBLC; Benoit-Bird and Au, 2006; Reid et al., 1991; Wilson and Boehlert, 2004). These animals migrate towards the surface and over shallow bathymetry each night presenting a distinct forage community for larger animals. This community is found close to shore over the 500–800 m contour during the day. It is not clear whether the islands also enhance the productivity of the oceanic micronekton community offshore of the boundary community zone through an island mass effect (Roger, 1986).

The predominant mesoscale oceanographic process in the Hawaiian islands is the formation of mid-ocean eddies (Calil et al., 2008). The influence of mid-ocean eddies on micronekton is not

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clear but bottom up or aggregation effects may occur because of enhanced primary and secondary production (Benitez-Nelson et al., 2007; Goldthwait and Steinberg, 2008; Rii et al., 2008). They are known to concentrate large fishes such as tuna (Murphy and Shomura, 1972; Owen, 1981; Sugimoto and Tameishi, 1992) and cetaceans (Davis et al., 2002; Olson et al., 1994).

Micronekton are, by definition, capable of swimming against currents. Most mesopelagic micronekton species undergo a diel vertical migration from depth during the day to shallower waters at night and then back. Migration patterns are finely tuned to light levels. Animals tend to follow a particular isolume which allows them to maintain bioluminescent counterillumination and simply to remain inconspicuous to predators under dim light (Kampa, 1971; Young, 1983). Some studies have found that the phase of the moon can alter their nighttime depth distributions (Hernandez-Leon et al., 2001; McManus et al., 2008). This implies that active behavior by these organisms, as well as physical processes in their environment, contribute to their distribution. To what extent such behavioral changes in distribution alter patterns observed spatially is unclear.

Here we assess spatial variability in micronekton abundance and biomass in Hawaiian waters in relation to oceanographic and bathymetric features. This field sampling was designed principally to assess the influence of Cross seamount on the oceanic micronekton (De Forest and Drazen, 2009). In the process, trawls were conducted from 2005 to 2008 at Cross seamount and opportunistically from a near island location (Keahole Pt), over Finch seamount, in the open ocean, and from the edge of a cyclonic mid-ocean eddy. A total of 58 trawls afford the opportunity to compare micronekton communities in Hawaiian waters. In addition, an examination of the influence of lunar illumination (moon phase) is conducted because the trawls were taken during different parts of the lunar cycle.

2. Methods

Samples were collected from three cruises during late April and early May of 2005, 2007, and 2008 aboard the NOAA research

vessel *Oscar Elton Sette*. A dual warp modified Cobb trawl was used for collection. The open mouth area was 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. In an attempt to reduce damage to specimens during the trawl, the cod-end of the net was modified for the 2007 and 2008 cruises. 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 was attached. It was constructed from plasticized canvas with dimensions of 30 cm diameter by 61 cm length.

We conducted two types of trawls: day-deep and night-shallow. Day-deep trawls were at depths between 400 and 650 m and night-shallow trawls were at depths between 0 and 200 m. Trawl depths were selected based on concurrently conducted acoustic surveys indicating the depths showing the greatest density of sound-scattering organisms. We fished each trawl for 60 min at depth at a speed of 3 knots. This resulted in approximately 802,600 m³ of water filtered per trawl. The data are given on a per trawl basis. 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 data to the ship via acoustic telemetry on latitude, longitude, temperature and depth. Unfortunately, this system behaved erratically often failing to report data or reporting data that was incorrect. In 2007 and 2008 a small TDR (time-depth recorder) was attached to the net in addition to the Netminds.

Several regions in the vicinity of the main Hawaiian Islands were sampled. Sampling areas were (1) at or near Cross Seamount, (2) over the summit of Finch seamount, (3) offshore of Keahole Point, in the lee of Hawaii Island, (4) an open-ocean site located between Cross Seamount and the island of O'ahu, and (5) at the edge of a cyclonic eddy located between Cross Seamount and the island of Oahu (Fig. 1). Cross seamount rises to 330 m and has a relatively flat plateau with a diameter of ~8 km. At or near Cross Seamount three types of trawls were conducted: summit, flank, and "away." Summit trawls ran directly over the flat-plateau summit in waters less than 500 m. No day-deep trawls were conducted over the summit because of the shallow bathymetry. Flank trawls ran alongside the

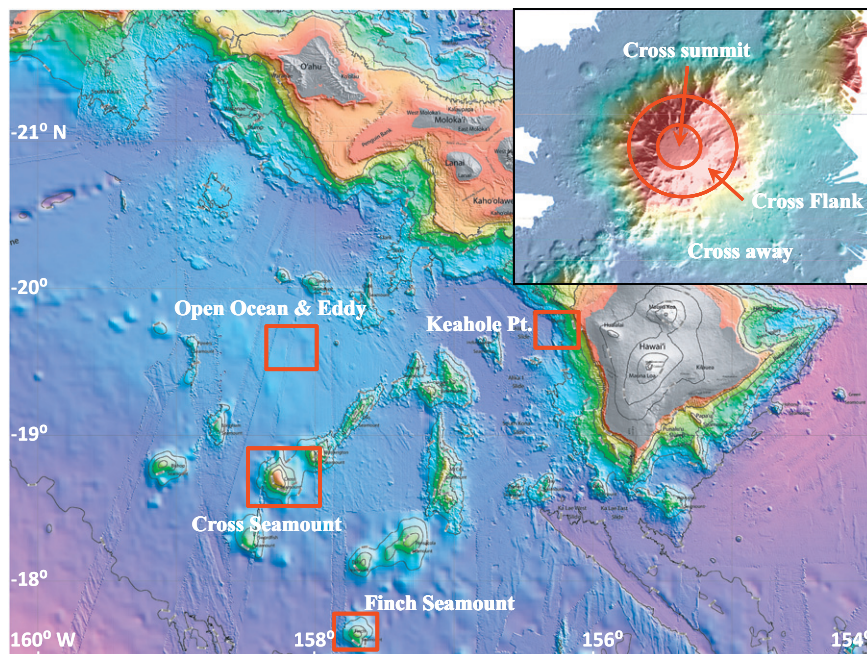


Fig. 1. Micronekton sampling sites around the Hawaiian Islands with an inset of Cross Seamount. Bathymetric image modified from Eakins et al. (2003) available at <http://geopubs.wr.usgs.gov/i-map/i2809>.

slopes immediately surrounding the summit in waters with bottom depths between 500 and 1500 m and were taken in 2007 and 2008 only. “Away” trawls were conducted in waters with bottom depths greater than 1500 m and < 14 km from the summit of Cross Seamount. Results from trawls in the vicinity of Cross seamount in 2005 and 2007 have already been reported elsewhere in detail (De Forest and Drazen, 2009) but the data are included in the present analyses for the purposes of comparisons to other sampling areas.

Finch seamount and Keahole Pt were sampled in 2005 only. Finch seamount is located southeast of Cross seamount and has a conical summit rising to 1000 m. It lies in the path of the westward flowing North Equatorial Current (NEC), outside of the influence of the Main Hawaiian Island (MHI) chain. On the other hand, Cross Seamount is located in the wake of internal tides and currents generated at the MHI, and can be influenced by a strong jet generated at the Southernmost point of the Hawaii Island by interactions of the NEC and topography. The area sampled offshore of Keahole Pt was in water depths greater than 2000 m and from 18 to 36 km offshore.

An open ocean site was sampled in all three years. During the 2005 and 2007 cruises there was no eddy activity in the regions sampled (as determined by sea-surface temperature and height). However, in 2008 a cyclonic eddy was present at the open ocean sampling station and the eddy edge was sampled. The eddy was approximately 140 × 200 km in dimensions and resulted in a 50 m upward shift of the depth of isotherms and isopycnals. However, the depth of Chlorophyll maxima shifted only about 25 m upward and stayed below the mixed layer depth, with no observable effects of the eddy on chlorophyll concentrations.

In the laboratory, all preserved specimens were sorted to the lowest taxonomic level possible, counted, and weighed. Large nekton were occasionally captured but were excluded from the analysis. Animals smaller than micronekton (2 cm), such as euphausiids, were excluded from analysis because they were not efficiently captured with the large mesh 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. Micronekton abundance and biomass, calculated on a per-trawl basis, were compared using one-way PERMANOVA with unrestricted permutations and type III sums of squares (Anderson et al., 2008). To avoid the problem of multiple comparisons associated with post-hoc testing we employed the method of Benjamini and Hochberg (1995) which minimizes the false discovery rate. In cases where the number of possible permutations was low (< 100) then the Monte Carlo approach was used to determine the significance of the *t* statistic (Anderson and Robinson, 2003). The individual uncorrected *p*-values for pair wise comparisons are given. Additionally, the relatedness of the communities sampled in each area was examined using ANOSIM on a Bray–Curtis similarity matrix computed using the square-root-transformed abundance data for all taxa from each trawl (PRIMER v6). Transformation was required because of the non-normal distribution of the variables, large number of zeros, and to reduce the influence of a few very abundant taxa (Clarke and Green, 1988). Subsequently, each significantly different group was compared using a SIMPER analysis that evaluated each taxonomic units contribution to the similarity within each group. Biomass generally was more variable within any given group but analysis of this data gave similar results so is not shown.

The effect of lunar illumination was examined. Moon phases (to within one quarter moon) were categorized as either new moon, half moon, and full moon using a moon phase calendar (<http://tidesandcurrents.noaa.gov/astronomical.html>). This product specifies moon phase, rise, and set times. In a few instances, the moon rose after or set before the trawl was conducted, by an

hour or more. For the purposes of these analyses, the moon phase for these trawls was considered new moon because we were interested in lunar illumination rather than tidal cycles or the potential for endogenous biological rhythms. However, we refer to the level of lunar illumination as moon phase as a convenient and simple way to describe relative light levels. The influence of lunar illumination on the micronekton were assessed using a two-way, crossed PERMANOVA (location and moon phase as fixed factors), with type III sums of squares (Anderson et al., 2008).

3. Results

A total of 58 trawl samples were collected in the vicinity of the Hawaiian Islands (Fig. 1). The distribution of these trawls amongst years and locations is given in Fig. 2. Abundance and biomass for the open ocean, Cross seamount summit, and Cross away sampling areas were available for both 2005 and 2007 but estimates were not statistically different between years (PERMANOVA, $p > 0.05$, see De Forest and Drazen, 2009) so these trawls were pooled for all subsequent analysis. They are referred to hereafter simply as Cross summit and Cross away for simplicity. As noted above, the opportunity to sample a mid-ocean eddy presented itself only in 2008 near the open ocean samples from 2005 and 2007. Keahole Point and Finch seamount were sampled in 2005 only.

Comparisons between trawl groups revealed more similarity than differences in micronekton abundance and biomass (Fig. 2, Table 1). Mean micronekton abundance in night shallow trawls was quite consistent at ~ 1000 trawl⁻¹ whereas mean biomass was much more variable. Amongst the night shallow tows three groups stand out—Cross summit, Keahole Pt, and the eddy. Cross summit had significantly lower abundance and biomass than many of the other areas and in comparison to abundance over the summit in 2008 (Table 1). Indeed, samples from the summit in 2008 were similar to samples taken from the flanks and other areas, except for Keahole Pt. Keahole Pt abundance was roughly twice that found at other locations (but significant after correction for multiple comparisons at Cross Away, Cross Summit, and Cross Summit 2008 only) with biomass being significantly higher than at Cross summit and Cross summit in 2008 (Table 1). The two eddy samples have a mean micronekton abundance similar to that at Keahole Pt but significantly greater than Cross summit only probably due to the low sample size.

Estimates of micronekton abundance and biomass in day-deep tows were lower than in night-shallows (Fig. 2). Abundance was relatively consistent with ~ 400 trawl⁻¹. As with the night-shallow trawls, biomass was more variable than abundance and no significant differences were found (PERMANOVA, $p = 0.13$ and 0.06 , respectively, Table 1). Qualitatively, Finch seamount had the lowest abundance and biomass and the eddy samples the highest.

Differences in community composition first were examined using broad groupings of taxa. Myctophids dominated the abundance (55–70%) and biomass (70–85%) of micronekton in night-shallow tows with other fishes, cephalopods, shrimp, and other crustaceans making up the remainder of abundance and biomass (Fig. 3). In contrast, at Cross seamount summit, myctophids were only 15% of the abundance and 33% of the biomass of the micronekton. Other fishes, principally juvenile epipelagic and reef fishes, and other crustaceans, principally large transparent stomatopod larvae, made up much greater proportions of the abundance. In addition to these two groups, cephalopods contributed to a much greater proportion of the biomass in this location. In day-deep tows, most of the abundance and biomass was other fishes, principally *Cyclothone* spp., *Sigmops ebelingi*, hatchetfishes, and the eel *Serrivomer* sp. (Fig. 3).

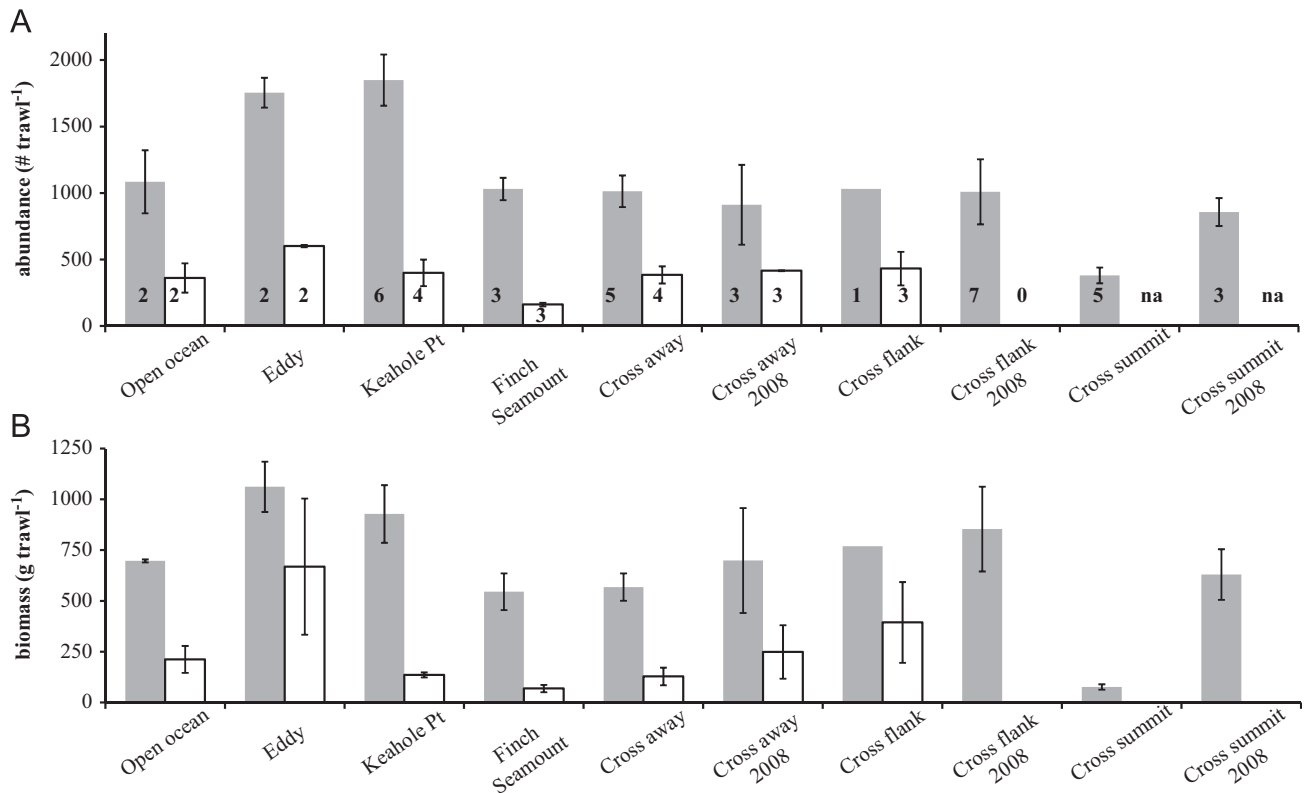


Fig. 2. Variation in night-shallow (gray bars) and day-deep (white bars) micronekton: (A) abundance and (B) biomass by sampling location and year (see text). Values are means and standard errors. Samples sizes are given in A, at the base of each bar.

Table 1

One-way PERMANOVA tests found significant differences for abundance and biomass in night-shallow (NS) trawls ($p < 0.001$ and $p < 0.05$, respectively). No significant differences were found amongst the day-deep (DD) samples ($p > 0.05$). Results of one-way PERMANOVA post-hoc comparisons between sampling locations and years are given below as p -values (all uncorrected values < 0.05 are given) with those that were significant after correcting for multiple comparisons in bold. The first number refers to differences in abundance and the second to biomass. C—Cross seamount and sum—summit.

| DD | NS | | | | | | | | | |
|-------------|------------|------|---------|----------------|--------------------------|----------------|---------|----------------|----------------------|--------------------------|
| | Open ocean | Eddy | Keahole | Finch | C away | C away '08 | C flank | C flank '08 | C summ | C summ '08 |
| Open ocean | X | | | | | | | | | |
| Eddy | | X | | | | | | | | |
| Keahole | | | X | 0.0308/ > 0.05 | 0.0071/ > 0.05 | 0.0234/ > 0.05 | | 0.0321/ > 0.05 | 0.0072/0.0001 | 0.0001/0.0001 |
| Finch | | | | X | | | | | 0.0044/0.0040 | 0.0111/ > 0.05 |
| C away | | | | | X | | | | 0.0008/0.0002 | 0.0008/0.0002 |
| C away '08 | | | | | | X | | | 0.0014/0.0001 | 0.0014/0.0001 |
| C flank | | | | | | | X | | 0.0365/0.0165 | |
| C flank '08 | na | na | na | na | na | na | X | | > 0.05/0.0136 | |
| C summ | na | na | na | na | na | na | na | X | | 0.0041/0.0011 |
| C summ '08 | na | na | na | na | na | na | na | na | | X |

Differences in community composition (based on abundances) were evident between some of the trawl groups (ANOSIM, global $R=0.66$, $p < 0.001$). No comparisons were possible to Cross flank in 2007 as there was only a single trawl. Cross summit, night-shallow samples were distinct from all other trawl groups (Table 2). As stated above, there were considerably fewer myctophids as well as fewer squids and mesopelagic crustaceans and these groups were the dominant contributors to the dissimilarity (Appendix A). It is interesting to note the mesopelagic boundary layer community (MBLC) members, the squid *Liocranchia reinhardi* and the myctophid *Benthosema fibulatum*, which were present in 2005 and 2007 were reduced considerably in abundance or absent in 2008. Instead, *Diaphus trachops*, another MBLC member, was present but also in 2008 Cross away samples. Keahole Pt night-shallow samples were

distinct from all others as well but because of increased abundances of individual taxa rather than the presence of different taxa. They had much greater abundances of many myctophids, notably *Ceratoscopelus warmingii* and *Diaphus schmidti*, as well as the shrimps *Sergia* spp. and *Sergestes* spp., stomatopods and a few squids such as *Abralia trigonura* (a MBLC member; Appendix A). Keahole Pt day-deep samples were distinct from Finch seamount, Cross flank and Cross away 2008 samples (Table 2). In this case the differences were driven by higher abundances of *Sergestes* spp., *Oplophorus gracilorostis* (a MBLC member), *Diaphus mollis*, *Lobiancha gamelleri*, *Argyropelecus* spp., and lower abundances of a few taxa such as *Hygophum proximum*, *Serrivomer* sp. and *Sigmops ebelingi* in Keahole Pt. samples (Appendix A). These community differences are in contrast to similar total abundances between these locations.

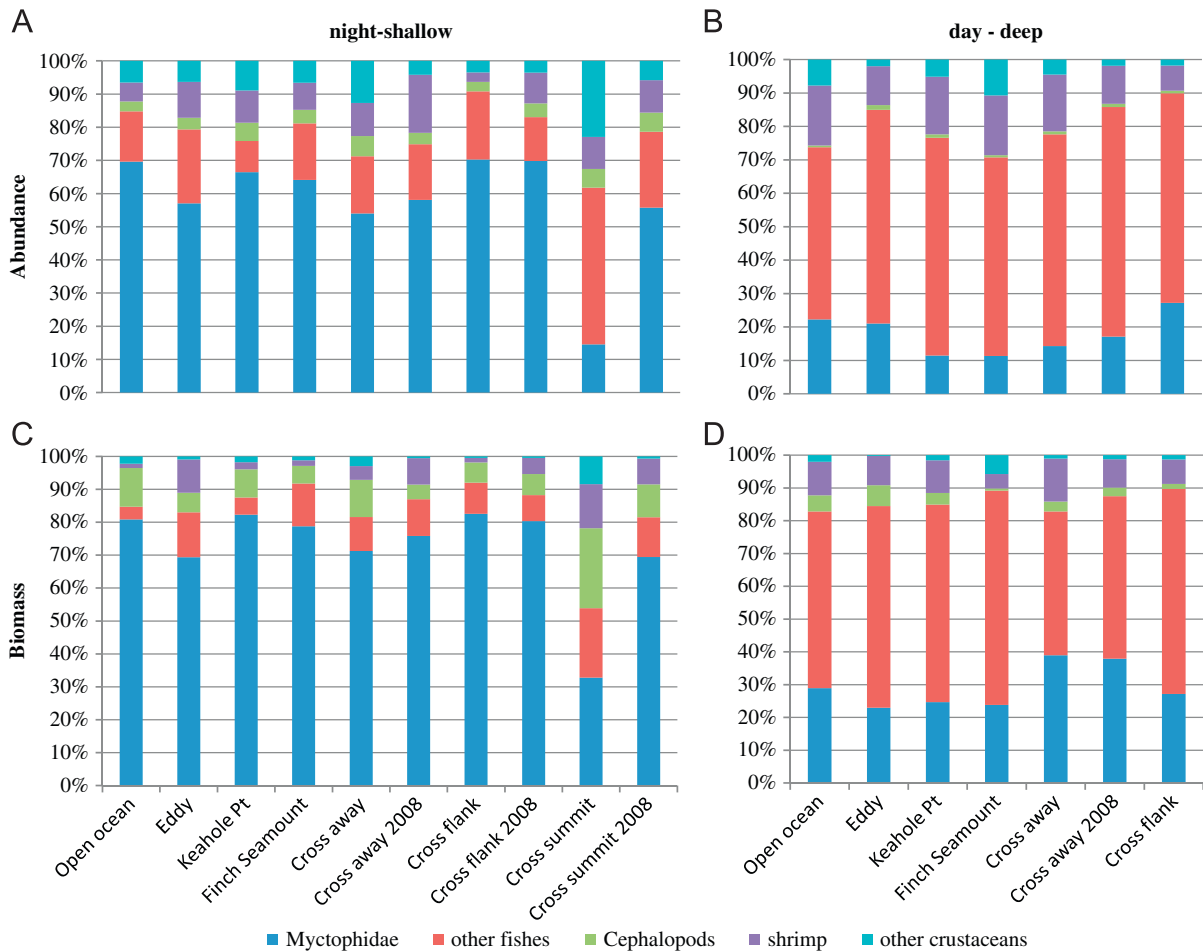


Fig. 3. Gross composition of micronekton abundance (A—night-shallow, B—day-deep) and biomass (C—night-shallow, D—day-deep).

Table 2

Results from SIMPER (numerical values=dissimilarity) and ANOSIM (bold values indicate significant differences, $p < 0.05$) between sampling groups. C—Cross seamount, sum—summit, NS—night shallow, and DD—day deep.

| DD | NS | | | | | | | | | |
|-------------|------------|-------|--------------|--------------|--------------|--------------|---------|--------------|--------------|--------------|
| | Open ocean | Eddy | Keahole | Finch | C away | C away '08 | C flank | C flank '08 | C summ | C summ '08 |
| Open ocean | X | 40.44 | 38.23 | 34.22 | 38.56 | 39.08 | 29.36 | 41.26 | 57.80 | 39.47 |
| Eddy | 52.81 | X | 42.19 | 41.56 | 40.56 | 38.39 | 37.80 | 39.34 | 67.16 | 31.98 |
| Keahole | 49.37 | 64.29 | X | 36.14 | 39.44 | 45.65 | 42.32 | 46.97 | 62.14 | 45.83 |
| Finch | 52.71 | 64.39 | 44.99 | X | 38.22 | 41.04 | 37.03 | 43.42 | 59.56 | 40.71 |
| C away | 47.23 | 55.37 | 45.37 | 49.57 | X | 40.16 | 36.90 | 43.30 | 59.11 | 38.44 |
| C away '08 | 48.46 | 41.52 | 55.90 | 57.80 | 49.94 | X | 37.54 | 38.28 | 58.09 | 30.72 |
| C flank | 50.22 | 47.74 | 59.55 | 58.26 | 53.57 | 50.04 | X | 39.80 | 58.62 | 35.75 |
| C flank '08 | na | na | na | na | na | na | na | X | 62.67 | 36.44 |
| C summ | na | na | na | na | na | na | na | na | X | 59.22 |
| C summ '08 | na | na | na | na | na | na | na | na | na | X |

In examining the data, it becomes apparent that lunar illumination had a strong effect on estimates of micronekton abundance and biomass in the nighttime samples (Fig. 4). In 2008, the summit of Cross seamount was sampled during a new moon for two of the three tows with much greater abundances than in 2005 and 2007 when the moon was half to full. The differences are not likely the result of fishing at different times of the night because tows in 2005–2007 commenced from 10 pm to 1:30 am and in 2008 the tows commenced between 9:45 and 12:30. For 2008, the flank samples are strongly affected by lunar illumination with new moon samples later in the cruise having twice the abundance as the samples at the start of the cruise with full or

half moon (Fig. 4). Similar results are evident for the Cross away samples too. The effect of lunar illumination on both biomass and abundance was highly significant (PERMANOVA; $p < 0.001$) as was location ($p < 0.05$). Finally, the Keahole Pt and eddy samples were taken during the new moon and had the greatest estimates of abundance in the data set. Indeed the differences in community composition between Keahole Pt and the other sampling groups (ANOSIM, $p < 0.05$) could be a location or illumination effect but it is not possible to differentiate these because all samples were taken during the new moon.

The sampling around Cross seamount (summit, flanks and nearby away groups) occurred across the lunar cycle and provides

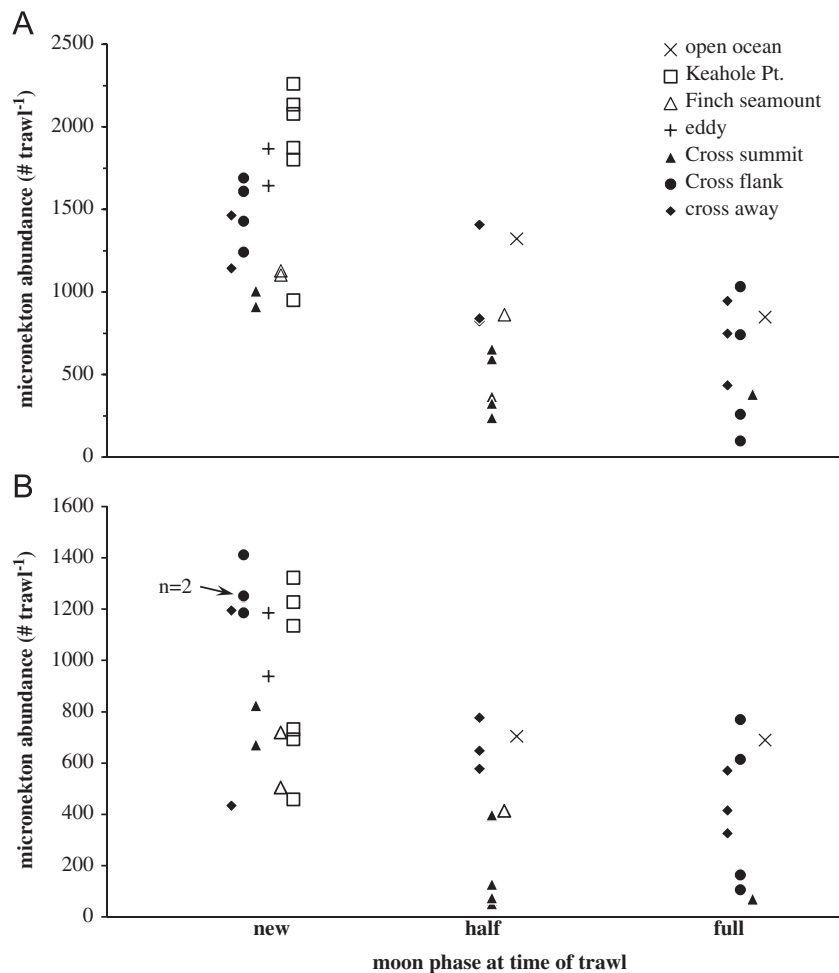


Fig. 4. Total micronekton (A) abundance and (B) biomass in night shallow tows as a function of moon phase (level of lunar illumination) at the time of each trawl.

Table 3

SIMPER results showing the 20 taxa contributing most to average dissimilarity (total = 55.7%) between new ($n=2$) and half/full ($n=6$) moon phase samples over Cross seamount summit. Each taxon's contribution to the total dissimilarity is given.

| Species | Abundance (# trawl ⁻¹) | | % of dissimilarity | cum.% |
|---------------------------------|------------------------------------|-------|--------------------|-------|
| | Half/full | New | | |
| <i>Diaphus schmidti</i> | 13.5 | 175.8 | 6.47 | 6.47 |
| <i>Vinciguerria</i> sp. | 9.9 | 81.5 | 3.98 | 10.45 |
| <i>Lampanyctus</i> spp. | 2.2 | 43.6 | 3.97 | 14.42 |
| <i>Ceratoscopelus warmingii</i> | 9.9 | 75.9 | 3.69 | 18.11 |
| <i>Hygophum proximum</i> | 5.7 | 51.0 | 3.17 | 21.28 |
| <i>Oplophorus</i> sp. | 0.5 | 26.8 | 3.03 | 24.31 |
| <i>Diaphus anderseni</i> | 0.3 | 20.7 | 2.67 | 26.98 |
| Unidentified juvenile fish | 121.0 | 77.3 | 2.65 | 29.62 |
| <i>Diaphus brachycephalus</i> | 2.5 | 19.8 | 2.52 | 32.15 |
| <i>Lobianchia gemellarii</i> | 0.3 | 15.8 | 2.38 | 34.52 |
| <i>Diaphus trachops</i> | 0.8 | 16.2 | 2.17 | 36.69 |
| <i>Diaphus fragilis</i> | 0.3 | 13.2 | 2.13 | 38.82 |
| Unidentified Myctophidae | 8.5 | 34.8 | 1.98 | 40.8 |
| <i>Bolinichthys longipes</i> | 0.5 | 10.4 | 1.96 | 42.76 |
| <i>Abrialopsis pacifica</i> | 1.3 | 15.7 | 1.86 | 44.61 |
| <i>Diaphus</i> sp. | 0.2 | 8.6 | 1.79 | 46.4 |
| <i>Diaphus mollis</i> | 2.0 | 16.9 | 1.78 | 48.18 |
| <i>Sergia</i> spp. | 0.8 | 9.4 | 1.77 | 49.95 |
| <i>Diaphus rolfbolini</i> | 0.0 | 7.3 | 1.73 | 51.68 |
| <i>Benthosema fibulatum</i> | 6.1 | 0.0 | 1.68 | 53.36 |

the opportunity to compare variations in community composition at particular sites. Abundance and biomass were not statistically different between half and full moon phases (PERMANOVA,

$p < 0.05$) so these samples were pooled for comparison to new moon trawls. SIMPER analysis gives an average dissimilarity between the two new moon samples and the six half and one full moon samples as 55.7%. The groups leading to this dissimilarity are given in Table 3 and with the exception of the myctophid *Benthosema fibulatum* and juvenile fishes all are more abundant in the new moon group. For the seamount flank samples in 2008 there was an average dissimilarity of 54.2%. All of the top 20 taxa leading to the dissimilarity were more abundant in the new moon group (Table 4). The new moon Cross away samples were 39.78% dissimilar to the half/full moon samples, much less than for the summit or flank areas. Most taxa were more abundant in new moon samples except for the myctophids *Hygophum proximum*, *Bolinichthys longipes* and *Diaphus brachycephalus* (Table 5).

4. Discussion

Micronekton abundance and biomass was quite consistent between the sample groups of this study (exceptions will be discussed below). The night-shallow fauna was dominated by myctophids and the day-deep fauna was dominated by gonostomatids, particularly *Cyclothone* spp. (Fig. 3). It is difficult to compare the biomass and abundance measured in this study with others because of differences in the nets used. The advantage of the large Cobb trawl used in this study is that it effectively captures the large and often agile micronekton that smaller nets often do not (Clarke, 1983; Reid et al., 1991). Some studies using

Table 4

SIMPER results showing the 20 taxa contributing most to average dissimilarity (total=54.2%) between new ($n=4$) and half/full ($n=3$) moon phase samples over Cross seamount flanks in 2008. Each taxon's contribution to the total dissimilarity is given.

| Species | Abundance (# trawl ⁻¹) | | % of dissimilarity | cum.% |
|---------------------------------|------------------------------------|--------|--------------------|-------|
| | Half/full | New | | |
| <i>Lampanyctus</i> spp. | 18.66 | 190.16 | 5.90 | 5.90 |
| <i>Diaphus schmidti</i> | 81.36 | 295.84 | 5.81 | 11.72 |
| <i>Ceratoscopelus warmingii</i> | 55.35 | 217.27 | 4.64 | 16.35 |
| <i>Vinciguerria</i> sp. | 10.30 | 69.22 | 3.16 | 19.51 |
| <i>Sergia</i> spp. | 0.67 | 31.47 | 3.00 | 22.51 |
| <i>Diaphus brachycephalus</i> | 0.00 | 19.71 | 2.71 | 25.22 |
| <i>Sergestes</i> spp. | 4.62 | 39.44 | 2.58 | 27.80 |
| Unidentified juvenile fish | 10.37 | 31.81 | 2.48 | 30.28 |
| <i>Hygophum proximum</i> | 7.78 | 42.51 | 2.35 | 32.63 |
| <i>Janicella spinacauda</i> | 2.82 | 27.98 | 2.31 | 34.94 |
| <i>Abraliopsis pacifica</i> | 1.32 | 20.98 | 2.17 | 37.11 |
| <i>Bregmaceros</i> sp | 0.34 | 15.92 | 2.13 | 39.24 |
| <i>Diaphus anderseni</i> | 2.40 | 23.04 | 2.01 | 41.25 |
| <i>Diaphus rolfbolini</i> | 1.00 | 16.40 | 1.92 | 43.18 |
| Stomatopod | 7.73 | 32.15 | 1.85 | 45.02 |
| Onychoteuthidae | 0.11 | 10.63 | 1.81 | 46.84 |
| <i>Diaphus mollis</i> | 3.84 | 22.75 | 1.72 | 48.56 |
| Melanostomiidae | 0.00 | 6.97 | 1.61 | 50.16 |
| <i>Bolinichthys longipes</i> | 13.69 | 36.97 | 1.59 | 51.75 |
| <i>Abraliopsis</i> sp A | 0.11 | 8.76 | 1.59 | 53.34 |

Table 5

SIMPER results showing the 20 taxa contributing most to average dissimilarity (total=39.8%) between new ($n=2$) and half/full ($n=6$) moon phase samples in Cross away trawls. Each taxon's contribution to the total dissimilarity is given.

| Species | Abundance (# trawl ⁻¹) | | % of dissimilarity | cum.% |
|---------------------------------|------------------------------------|-------|--------------------|-------|
| | Half/full | New | | |
| <i>Lampanyctus</i> spp. | 63.5 | 67.4 | 4.63 | 4.63 |
| <i>Ceratoscopelus warmingii</i> | 76.2 | 196.0 | 3.73 | 8.36 |
| Stomatopod | 32.0 | 74.6 | 3.59 | 11.95 |
| <i>Diaphus schmidti</i> | 122.8 | 174.0 | 2.9 | 14.84 |
| <i>Diaphus anderseni</i> | 0.7 | 17.7 | 2.79 | 17.64 |
| <i>Hygophum proximum</i> | 35.9 | 25.1 | 2.68 | 20.32 |
| <i>Janicella spinacauda</i> | 29.2 | 37.3 | 2.66 | 22.98 |
| <i>Diaphus mollis</i> | 6.1 | 33.8 | 2.5 | 25.48 |
| crab megalops | 9.8 | 28.1 | 2.05 | 27.53 |
| <i>Sergia</i> spp. | 6.1 | 14.0 | 1.98 | 29.51 |
| Unidentified juvenile fish | 46.8 | 89.5 | 1.98 | 31.49 |
| <i>Abraliopsis</i> sp A | 2.8 | 12.5 | 1.97 | 33.46 |
| unidentified crustacean | 1.0 | 6.5 | 1.95 | 35.41 |
| <i>Vinciguerria</i> sp. | 39.8 | 74.0 | 1.95 | 37.36 |
| <i>Cyclothone</i> sp | 0.0 | 5.2 | 1.81 | 39.17 |
| <i>Abraliopsis pacifica</i> | 5.2 | 17.5 | 1.78 | 40.95 |
| <i>Sergestes</i> spp. | 30.6 | 57.9 | 1.74 | 42.69 |
| <i>Bolinichthys longipes</i> | 19.9 | 14.0 | 1.72 | 44.41 |
| <i>Diaphus brachycephalus</i> | 8.0 | 4.5 | 1.66 | 46.07 |
| <i>Bregmaceros</i> sp | 2.2 | 5.2 | 1.59 | 47.66 |

the same types of nets can be compared in terms of community composition and generally, these have found the same gross community composition. Clarke (1983) used a similar Cobb trawl when sampling the region in the lee of Oahu and found a community dominated by myctophids. Reid et al. (1991) also found myctophids to numerically dominate the night-shallow community surrounding the Hawaiian Islands with shrimps, primarily sergestids, and a few cephalopods also captured. Maynard et al. (1975) provides the only other community analysis of micronekton in the region but it was described from small IKMT net tows. In this case, sergestid and penaid shrimps were the most abundant components of the community, followed by myctophids, euphausiids, caridean shrimps, and gonostomatids.

These differences likely reflect different capture efficiencies of the nets.

Keahole Pt stood out from the other sampled areas in having twice the night-shallow abundance (significant in three cases) and qualitatively greater biomass than the other areas (Fig. 2). These differences were evident in the myctophid fishes, squids, and shrimps. All night trawls offshore of Keahole Point were taken at 0–200 m depth at least 18 km from the shoreline in waters with bottom depths greater than 2000 m. The SIMPER analysis found differences between Keahole and other trawl groups but primarily because of large increases of several taxa rather than absences or additions of taxa. It seems that the samples represent an abundant fauna very similar to that found in the other sampling areas. Several MBLC members were present in higher densities than the other sampling areas (but not significantly so) which were further from the islands, but none contributed greatly to the overall abundance or biomass (Appendix A)). The MBLC species included the squid *Abralia trigonura*, the shrimps *Janicella spinacauda* and *Oplophorus gracilorostris*, and the myctophid *B. fibulatum*. These results are not surprising considering the proximity of the sampling site to the island of Hawaii. The relatively high abundance and biomass of the night trawls offshore of Keahole Point may be the result of local nutrient enrichment, called the island-mass effect (Roger, 1986). Cyclonic upwelling eddies regularly form in the lee of Hawai'i Island (Calil et al., 2008), and could stimulate micronekton abundance and biomass found there from bottom-up effects (see also below). The nature of the eddies' influence on micronekton and the duration of their potential effects are not known but no eddies were present during our sampling of this site in 2005. If such bottom-up mechanisms were responsible then a greater abundance and biomass of the micronekton would be expected at their daytime residence depths. The fauna was different at depth compared to some of the other areas (ANOSIM; $p < 0.05$) having greater numbers of some shrimps and fishes and lower abundances of others but overall abundance and biomass were not significantly greater than the other sample groups (Fig. 2). This strongly suggests an alternate mechanism such as lunar illumination, which will be discussed in more detail below.

The few trawls from a cyclonic mid-ocean eddy are intriguing in that they suggest these features lead to increased micronekton abundance and biomass. High abundances and biomasses were found in both day deep and night shallow tows although with sample sizes of two each significant differences were in comparison to Cross seamount summit only (Table 1). Concurrence between the night-shallow and day-deep tows lends some weight to the conclusion that an eddy was responsible for the trends seen and suggests that the pattern is could be spatial and not related to changes in migration patterns arising from taking these tows during the new moon (see also below). 6–9 cyclonic eddies form in the lee of Hawaii Island each year (Calil et al., 2008). Recent work has found that the circulation and upwelling results in increased nutrients, primary production and as much as an 80% increase in zooplankton abundance (Benitez-Nelson and McGillicuddy, 2008; Brown et al., 2008; Landry et al., 2008). SeaWiFS and MODIS sea surface color information show no anomaly in chlorophyll but it is possible that the zooplankton response to this eddy was large enough to result in enhanced feeding opportunities for the micronekton and persisted long enough to attract micronekters from the surrounding ocean. Eddies have been suggested to alter the distribution of marlin and other billfish in the lee of Hawaii island (Seki et al., 2002) and can alter the distribution of predators in other ocean regions (Davis et al., 2002; Domokos et al., 2007). Clearly four trawls are not adequate to conclusively assess the effect of mid-ocean eddies on the micronekton. However, our results are suggestive and they point out the need to evaluate the influence of mid-ocean eddies on mid-trophic levels.

Cross seamount has a strong influence on the micronekton community. De Forest and Drazen (2009) compared the micronekton over the summit of the seamount to stations along the flanks and away from the seamount (Cross away group) and found significant reductions in micronekton biomass and abundance over the summit. Most of the migrating myctophids, shrimps, and squids are either absent or much reduced in abundance which significantly altered the community composition (Fig. 3). Here we compare the micronekton community to other areas in Hawaiian waters and to trawls around the seamount collected in 2008. Finch seamount with its 1000 m deep summit, below the daytime depths of most micronekton, had a night-shallow abundance significantly higher than Cross seamount summit. The variable effect of seamounts on the pelagic fauna has been attributed to seamount summit depth in relation to daytime depth of the zooplankton and micronekton in other studies (Porteiro and Sutton, 2007). Cross summit had significantly lower abundance and/or biomass compared to Keahole point, the open ocean and Cross away samples. There was lower abundance and biomass at Cross away and flank 2008 samples as well but these were not significant after corrections for multiple comparisons (Fig. 2; Table 1). These results further confirm the strong influence of Cross seamount on the micronekton. Tuna-diet studies have indicated that bigeye caught over the Cross Seamount have fuller stomachs than those caught away from the seamount (Holland and Grubbs, 2007). Benthopelagic fishes that are micronekton predators, such as monchong (*Eumigistus illustris*) and alfonsinos (*Beryx splendens*), are also found in abundance over Cross Seamount. Active avoidance of the seamount by the micronekton may be occurring. Micronekton may avoid the summit because of the presence of hard substrate as well as the increased predator abundance. The summit of Cross Seamount is 330 m below the sea surface at its shallowest. All the micronekton taxa that are completely absent over the summit have average daytime depths ≥ 500 m. Those taxa that are still present over the summit, though reduced in numbers, have shallower daytime depths, generally between 200 and 500 m (De Forest and Drazen, 2009).

Perhaps the most interesting result from the 2008 seamount sampling is that micronekton abundance and biomass over the summit was not lower than away from the summit or the open ocean sites. In fact, the abundance over the summit in 2008 was significantly greater than that in 2005/2007 despite both sets of samples being collected during the spring (April/early May). The major environmental change in 2008 was that the summit was sampled during a new moon whereas the moon was roughly half or full in 2005 and 2007. Light is the well established proximate cue for animal vertical migration. Migratory zooplankton and micronekton seek a particular isolume at which they can remain concealed from predators and follow this isolume into surface waters as the sunsets (Hays, 2003). Lunar light alters the depth of these isolumes at night and it has been shown to effect individual animal vertical distributions such that krill (Tarling et al., 1999), sergestids (Walters, 1976), myctophids (Clarke, 1973), and predatory stomiatoids (John, 1978) are found deeper at night during a full moon. Hernandez-Leon et al. (2001) found that, during full moons, reduced micronekton abundances in surface waters at night likely reduced predation intensity on the zooplankton resulting in greater abundances of zooplankton. Our results show that the level of lunar illumination significantly influences estimates of total micronekton abundance and biomass in surface waters (0–200 m) at night (Fig. 4). We want to emphasize that we did not examine the lunar cycle per se which has been shown to be important to micronekton migration patterns through apparent endogenous rhythms, at least for micronekton moving inshore to water columns less than 150 m (Benoit-Bird et al., 2009).

Taking into account our crude measure of illumination, it seems a very plausible explanation for the higher abundance and biomass of micronekton at Keahole Pt in night shallow samples but not in day-deep ones. Lunar illumination also mediates the influence of Cross seamount on the micronekton community.

Sampling at Cross seamount occurred over the lunar cycle and significantly greater micronekton abundance was found during the new moon. No differences were found between the half and full moon suggesting that even partial lunar illumination is enough to alter the behavior of the micronekton. The effect was seen over the summit, along the flanks, and to a lesser degree in the waters away from the seamount. Three possibilities exist to explain the change in micronekton abundance over the seamount summit specifically. During the new moon the migrating micronekton may move closer to the sea surface and over the seamount itself. Certainly many species which were not seen over the seamount during half and full moons (De Forest and Drazen, 2009) were present during the new moon phase. From the SIMPER analyses the fishes *Diaphus schmidti*, *Vinciguerria* sp., *Lampanyctus* spp., *Ceratoscopelus warmingii*, *Hygophum proximum* led to the greatest dissimilarity between the moon phases. These species have vertical distributions from depths of ~ 500 –1000 m during the day to depths of 0–150 m at night (Clarke, 1973, 1974). Clarke (1973), using depth stratified tows of a Cobb trawl and an IKMT examined changes in the vertical distributions of many of these myctophids as a function of moon phase from the surface to 190 m depth. Species such as *Benthosema suborbitale* and *Diaphus schmidti* migrated to within 25 m of the sea surface during new moon but only came as shallow as 75–100 m during a full moon. For *D. schmidti* and two other *Diaphus* species he noted several times lower abundance during the full moon. *Lampanyctus niger* were found deep, > 145 m, during the new moon but were absent from his tows to 190 m during the full moon. Other species such as *L. steinbecki* and *L. nobilis*, also common in our samples, were found as shallow as 60–80 m during new moon but then only at depths > 150 m during full moon. Lastly, *C. warmingii* were most abundant at 15–100 m during new moon and at depths of 100–170 m during full moon but only at half the new moon abundance suggesting the rest of the population was even deeper.

Changes in avoidance between moon phases might also explain the trends. In many cases, Clarke's (1973) trends for the same species considered here were not explained by greater net avoidance during full moons because size frequencies were similar between moon phases indicating that larger more mobile individuals were not avoiding the net. The average myctophid mass obtained by dividing each trawl's myctophid abundance by its biomass showed no difference in myctophid size between the flank samples taken during the new and full moons ($p < 0.05$) and the average myctophid size was actually greater (1.05 vs. 2.15 g fish $^{-1}$) though not significantly so, during the half moon trawls over the summit. In addition, avoidance is an unlikely explanation for the present results because the differences between new and full moon are more pronounced over the seamount compared to the flanks and away locations. Avoidance should not vary regionally but migration patterns should be affected by the seamount summit.

A third hypothesis is that, during the new moon, visual predators such as tuna, which were hypothesized to be responsible for the low micronekton abundance over the seamount (predation hole), are less successful. The lack of predation would then be seen as higher micronekton abundances. Bigeye tuna vertical movements are correlated with lunar illumination with nighttime depths deeper during the full moon (Musyl et al., 2003; Schaefer and Fuller, 2002). This suggests that they are tracking the depth of micronekton layers but the differences in depth distribution are very small (~ 25 m) compared to very large shifts in

distributions of the micronekton (50–100 m; Clarke, 1973, 1974). Mesopelagic shrimps formed a substantial part of the diet of bigeye tuna over Cross seamount (Holland and Grubbs, 2007) and these taxa were much more abundant during the new moon over the summit (Table 3). An examination of the diet of tunas over the seamount in relation to the lunar cycle and levels of lunar illumination is needed to resolve this hypothesis. Regardless of the mechanism responsible for changing the micronekton patterns, it is very important to note that the influence of the seamount changes with the level of lunar illumination, a factor that must be taken into account when examining trophic relationships in this environment.

The members of the MBLC present over Cross seamount varied between years. Two members of the MBLC, the squid *Liocranchia reinhardti* and the myctophid *Benthosema fibulatum*, were found over Cross seamount in 2005/2007 (De Forest and Drazen, 2009). In 2008, *B. fibulatum* was absent and *L. reinhardti* was at low abundances similar to other areas sampled away from the island flanks. In contrast, *Diaphus trachops* was found in 2008 over the summit and in Cross away stations but the abundances varied greatly between individual trawls. None of the MBLC was found in elevated abundances over Finch seamount, which has a summit 1000 m deep, well below the daytime depths of this fauna between 500 and 800 m (Reid et al., 1991). The variable occurrence of some MBLC members and the lack of many others normally found along the flanks of the main islands suggest that Cross seamount presents a distinct environment not conducive to all of the MBLC. The islands may have greater productivity in nearshore waters supporting the MBLC because data from all three-field samplings at Cross Seamount have not detected significant increases in Chlorophyll *a* concentrations (Domokos, unpub. data). It is also possible that recruitment to isolated seamounts such as Cross is sporadic increasing resident community variability. Furthermore, studies of the Hancock seamounts to the northwest show a lack of larval retention of seamount associated species (Boehlert and Mundy, 1993; Boehlert et al., 1994). In any case, the MBLC species found at Cross seamount do not seem to form a consistent seamount associated fauna as has been found over other seamounts (Parin and Prutko, 1985; Porteiro and Sutton, 2007; Wilson and Boehlert, 2004).

In conclusion, the results presented here show that lunar illumination, Cross seamount and perhaps mid-ocean eddies alter micronekton abundance, biomass, and/or community composition. Mid-ocean eddies are widespread and common features of many ocean regions (Benitez-Nelson et al., 2007; McGillicuddy et al., 2007) and given our preliminary results on their positive effect on mesopelagic micronekton abundance and biomass, these locations may intensify food-web interactions. The present results are the first to examine the influence of the lunar illumination in conjunction with a seamount. Seamounts are now well known to alter micronekton distributions and abundances through behavioral and top-down trophic forcings (De Forest and Drazen, 2009; Porteiro and Sutton, 2007; Pusch et al., 2004). Our results suggest that the influence of moonlight on diel migration patterns is also important to understand and should be evaluated on other seamounts. These results provide a better understanding of the processes affecting mesopelagic micronekton distributions, prey for large commercially important nekton such as tunas and swordfish, and may help develop regional food-web models.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.dsr.2011.03.002.

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