FINE SCALE MOVEMENT OF THE LUSTROUS POMFRET (*EUMEGISTUS ILLUSTRIS*) AT CROSS SEAMOUNT

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Abstract

Aggregations of fish are believed to be supported by trophic subsidizing mechanisms resulting from bio-physical interactions at seamounts that lead to increased micronekton abundances or concentrations. Tracking individual fish behavior is one way to prove this is occurring however until recently tagging studies have not been conducted for deep seamount fish species. Using advanced acoustic and archival tags we successfully tagged *Eumegistus illustris* individuals inhabiting an isolated Hawaiian seamount at depths down to ~600m. We tracked 26 individuals and compared their movements to existing micronekton surveys at Cross Seamount in the context of feeding ecology and accepted trophic subsidizing mechanisms and estimated residence time. Fish displayed strong diel vertical migration behavior, swimming into the water column at night at depths consistent with feeding on mesopelagic boundary community micronekton and became primarily benthic associated around dawn as the shallow scattering layer compressed along the summit of the seamount. Depth distributions varied between individuals. One individual with an archival tag left the seamount after being tagged and remained away for 90 days suggesting movement between isolated habitats is possible. Fish had a strong association with the seamount and were present 97% of the days they were tracked, on average. Average residence time was 103 days (*SD* = 162) but this was confounded by indications of high post release mortality.

Introduction

Mechanisms of trophic subsidy to seamounts

At seamounts, bio-physical interactions often result in localized increased micronekton abundances and support aggregations of seamount-associated fish (Genin 2004, Koslow 1997, Porteiro and Sutton 2007, Fock 2002). Diverse processes can increase abundance or concentration of prey species in an otherwise diffuse foraging area and support aggregations of benthopelagic fish (Parin & Prut'ko 1985, Porteiro and Sutton 2007). Mechanisms that can subsidize available micronekton biomass to higher trophic levels on seamounts and support aggregations of seamount-associated fish include 1) diel vertical migration 2) feed-rest behavior 3) topographic blockage and 4) presence of mesopelagic boundary communities.

Diel vertical migration (DVM) behavior is a feeding and predator avoidance strategy observed in an abundance of marine organisms from zooplankton to large fish and in a variety of pelagic and non-pelagic environments including seamounts (Sims et al. 2006, Polovina et al. 2008, Comfort 2015, Sassa 2002, Gauthier 2002, Afonso 2014). Every night deep scattering layer (DSL) zooplankton and micronekton ascend in mass to feed in more productive shallow waters and form the shallow scattering layer (SSL). Over the summits seamounts may have either pronounced or depleted SSLs in comparison to nearby pelagic waters and they often contain unique seamount associated species (DeForest & Drazen 2009, Genin 2004, Boehlert 1988). Mesopelagic predators undergoing DVM at seamounts can be provided unique feeding opportunities with potentially abundant forage but little is known about the relative importance or individual variability of this mechanism (Afonso 2014).

Currents bringing a high flux of zooplankton and micronekton are often enhanced around bathymetric features providing food for resting fish. The feed-rest hypothesis predicts that fish can energetically benefit by taking refuge in pockets of low current, protected by the bathymetric structure of a seamount or other bathymetric feature and save energy that would otherwise be expended swimming (Tseytlin 1985, Genin 2004, Morato 2009). Genin and Dower (2007) suggested that this feeding mechanism is vital for orange roughy (*Hoplostethus atlanticus*)—a fish often found aggregating at deep seamounts with high currents. This mechanism occurs similarly at shallower seamounts but a wider array of trophic subsidies and feeding opportunities may reduce its relative importance.

Topographic blockage, predicts that diel vertically migrating micronekton that ascend to shallower water at night to feed, move laterally with currents and may be blocked upon descent by protruding bathymetry and become trapped, providing a dense later of forage for predators (Isaacs & Schwartzlose 1965, Genin 2004). This mechanism is most likely to provide an important energetic component to the diet of predators at seamounts with fast currents and large summits between the DSL and SSL (Genin 2004).

Micronekton communities often display distinct behaviors and appear at greater abundances around seamounts and deep slopes than adjoining pelagic environments and may provide unique foraging opportunities. Mesopelagic boundary communities (MBCs) consist of micronekton, including species unusual to pelagic waters, that spend the day associated with slopes and seamount flanks at concentrations greater than nearby pelagic waters often ascending into the water column at night (Boehlert and Seki 1984, Parin & Prut'ko 1985, Boehlert and Genin 1987, DeForest & Drazen 2009, Reid et al. 1991). Over seamounts micronekton distributions throughout the water column can be unique and may provide a niche for predators to exploit that are absent in the open ocean. Juvenile bigeye tuna (*Thunnus obesus)* experienced a significant feeding benefit at Cross Seamount compared to adjacent pelagic waters by preying on mesopelagic boundary community micronekton (Holland & Grubbs 2007). Bigeye tuna are able to adequately feed in the often-lower prey densities of pelagic waters but other species may not have that ability and are dependent on the seamount habitat to provide the necessary energetic requirements (Genin 2004).

These four trophic subsidies have been observed independently using sonar, remotely operated vehicles, trawling surveys and stomach content analysis but few studies have taken a broad approach that can monitor detailed individual variability in behavior and combination of multiple mechanisms (Afonso 2014). By observing fine scale vertical and horizontal movements in relation to observed micronekton distributions it is possible to determine which trophic subsidizing mechanisms are important to the feeding ecology of these mesopelagic predators.

Micronekton dynamics at Cross Seamount

The phenomenon of enhanced micronekton abundance over seamounts has been repeatedly observed in Hawaiian waters (Boehlert and Seki 1984 , Sassa et al. 2002, Porteiro & Sutton 2007). Some micronekton species are able to actively hold position over seamounts in strong currents (Wilson and Boehlert 2004) and even swim against them upon descent (Domokos 2008). Cross Seamount has a micronekton regime distinctive from adjoining pelagic waters and taxonomically distinct seamount associated micronekton species may occur as a mesopelagic boundary layer community along the flanks of Cross Seamount during the day (Drazen et al. 2011). Bioacoustics surveys have identified a higher abundance of micronekton in the entire water column over Cross Seamount at night relative to pelagic waters only a few kilometers away with a conspicuous SSL in the top 200m and thick micronekton aggregations just over the seamount summit (Johnston et al. 2008, Domokos 2008, **Figs 1A and 1B**). This community, comprising higher biomass than pelagic waters, is likely sustained by the influx of planktonic organisms that are unable to swim against strong currents impinging on the seamount.

Additionally, a relatively thick deep scattering layer (DSL) on the flanks of Cross Seamount and extending 2-5 km away has been identified and likely consists in part of a taxonomically distinct mesopelagic boundary community (Domokos 2008). Typically in pelagic waters of this region, deep and shallow scattering layers consist of diverse assemblages between 20-200m and 500-800m depth respectively (Domokos 2009).

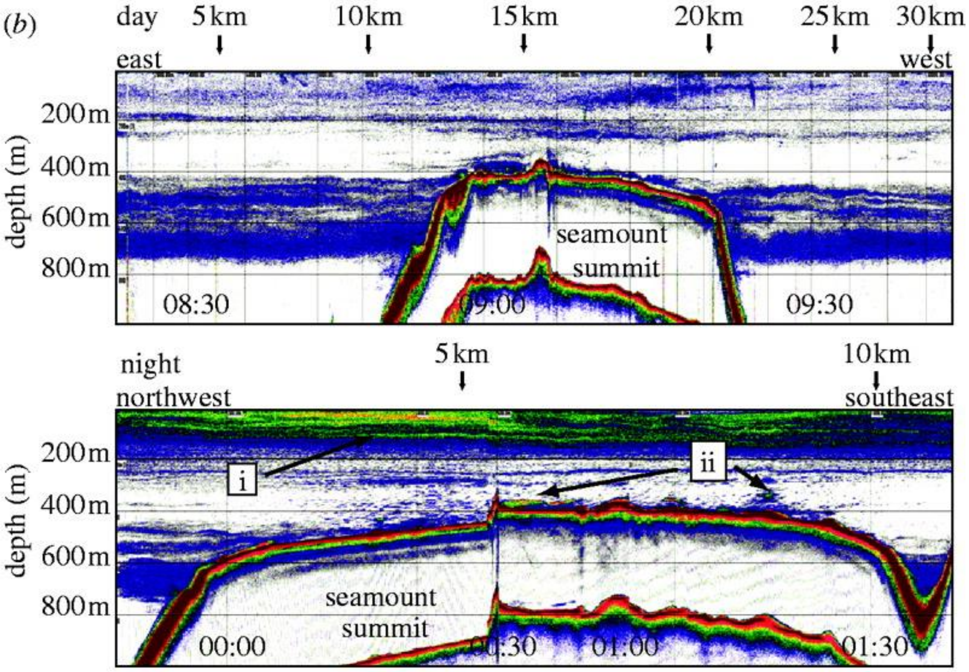

Figure 1A: Micronekton at Cross Seamount
Day and night echogram snapshots illustrating the nocturnal enhancement of prey fields (i and ii) at Cross Seamount. *(Figure and description from Johnston et al. 2008)*

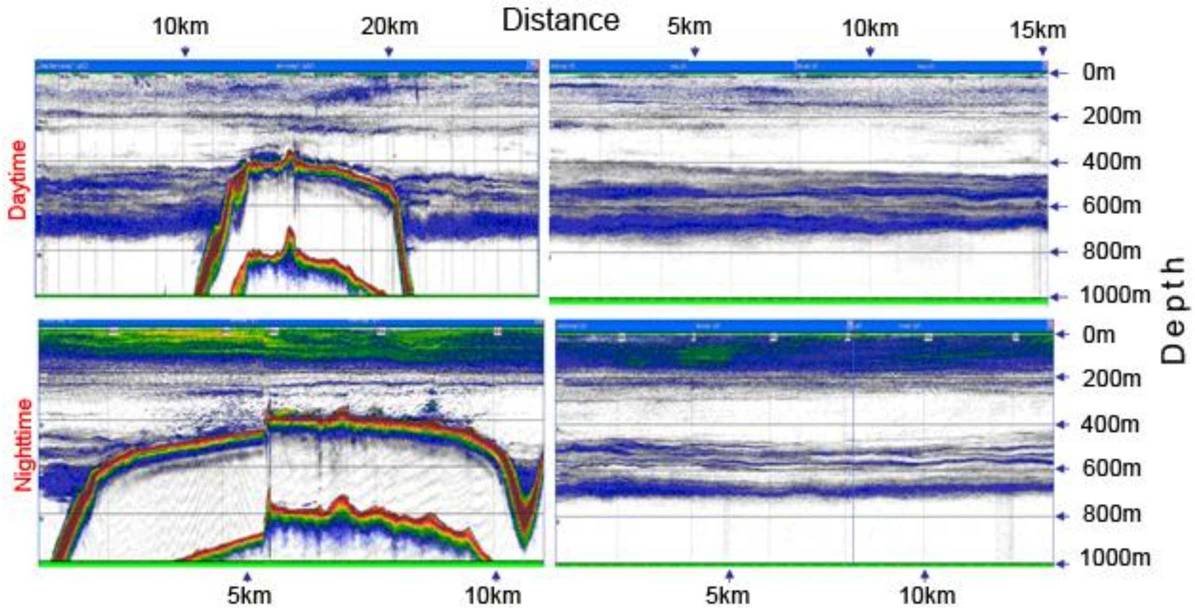

Figure 1B: Micronekton at and away from Cross Seamount
Acoustic backscatter data collected at Cross Seamount (left) and in the open ocean (right) show the aggregation of small organisms over the plateau of the seamount during both day (top panel) and night (bottom panel). *(Figure and description from Domokos, PIFSC Report to the Western Pacific Fishery Management Council June 2007).* The red and yellow lines represent the seamount summit. The blue color indicates the location of micronekton which is especially thick in green areas.

Abundant information on micronekton movement over Cross Seamount was collected on a series of NOAA cruises to Cross Seamount between 2005 and 2008. Data was collected with three frequencies of advanced split-beam acoustic sounders to monitor micronekton and fish movements and goals included characterizing oceanographic characteristics and micronekton community spatial dynamics and how they relate to micronektivorous fish. Much of the data collected from these cruises, some of which is summarized in the following two paragraphs, has not yet been published and was available via reports from Advanced Sampling Technology Workshop Group (ASTWG), Joint Institute for Marine and Atmospheric Research (JIMAR) and the Western Pacific Fisheries Management Council (WPFMC) from 2007-2010.

Located within the North Equatorial Current, Cross Seamount has unique oceanographic characteristics that increase biomass and support unique micronekton distributions. The seamount is influenced by internal tides produced by the Main Hawaiian Islands. It has a primarily anticyclonic flow and occasionally switches to a cyclonic flow, but when currents exceed 40 cm/sec no rotational flow is observed in the upper 200m of the water column. Taylor cones were often observed over the summit of the seamount, to ~200 m above the seamount summit but this flux of water was not enough to bring nutrients into the euphotic zone and enhance primary productivity. The impinging currents and advection of water over the seamount from the anticyclonic flow appeared to supply a flux of zooplankton to the seamount environment subsidizing forage for increased micronekton biomass, which in turn support greater numbers of individuals of higher tropic levels. Micronekton biomass was greater over the seamount and at the flanks compared to the pelagic environment a few kilometers away. In a daily cycle beginning at midnight the biomass would be greater over the summit of the seamount than over the flanks until 1800 hours at which time diel vertically migrating micronekton would ascend up over the flanks of the seamount and temporarily have greater concentration at the edges of the seamount. By 2000 hours the micronekton moved over the summit and once again biomass would be greater. In addition to greater biomass over the seamount than away from it at 20-200m depths, micronekton layers could be observed forming in depths 200-400m which is an area largely absent of micronekton in the pelagic. At the flanks of the seamount dense micronekton patches aggregated ~700-800m and increased micronekton concentrations often extended down the slopes to beyond 900m.

Vulnerability of seamount fisheries

Although fewer than 200 seamounts had been biologically surveyed by 2010 (Etnoyer 2010), seamount fish have a history of unsustainable exploitation and destructive fishing practices (Koslow 2000, Niklitschek 2010, Foley 2011, Clark 2000, Clark & Koslow 2007, Clark 2009, Clark 2010, Roark 2009, Williams et al. 2010). Many seamount-aggregating fishes have biological characteristics that make them intrinsically vulnerable to overfishing (Morato & Clark 2007, Morato 2006, Koslow 1997). Most targeted seamount associated species are 'K' selected with high longevity, late maturity, low natural maturity, low fecundity and sporadic recruitment giving them a very low sustainable yield on the order of 1-2% per year (Morato 2006, Koslow 2001, Koslow 1996, Koslow 1997).

As near shore fisheries become less productive, fishermen are looking to deep-water stocks for new fishing opportunities but overexploitation is common in commercial fisheries on seamounts (Clark 2000, Niklitschek 2010). The first seamount fishery for pelagic armourhead by soviet trawlers enjoyed landings as high as 200,000 tons a year but ended in commercial extinction of the species only 15 years after the fishery developed (Koslow 2001). Allegedly sustainable fisheries for orange roughy, such as Chatham Rise in New Zealand, may be sustained by continued discovery of new fishing grounds and subsequent serial depletion (Koslow 2001) and reductions of Patagonian toothfish in the Southern Ocean have been obscured by range expansions of the fishing fleet (Lord et al. 2006). In Ireland, there was a rapid boom and bust in a subsidized orange roughy fishery, and in a span of only 5 years after opening, the fishery closed. Economic analysis suggests that without government aid the fishery would never have been economically viable (Foley 2011). Given the life history characteristics of deep-sea fish, high costs of vessels, gear and fuel and the remote nature of seamounts and deep slopes, deep-sea commercial fisheries for many popular food fish may not ever be both economically and ecologically sustainable (Roberts 2002).

Regardless of life history characteristics, fish at an isolated habitat can be vulnerable to overexploitation at high fishing pressure and can have variable recruitment leading to slower recovery and greater susceptibility to overfishing (Myers & Pepin 1994). As an extreme example a hook and line fishery operating at depths ~90m was able to remove 82% of fish biomass from an isolated bank, consisting mostly of *Pristipomoides filamentosus,* in only 13 days (Grandcourt 2003). Even small to medium scale fisheries can be expected to have lasting impacts on local fish stocks and concentrated fishing effort can leave seamount fisheries highly vulnerable to overexploitation (Menezes 2013, Fry 2006).

In the late 1970's a handline fishery in the Hawaii EEZ began over Cross Seamount to target juvenile bigeye tuna aggregations and eventually developed a new fishing technique targeting pomfret. This 'shortline' fishing method was originally developed to target tuna but with slight modifications it could catch large numbers of pomfrets (**Fig S1,** Beverly 2004*).* Shortline fishing uses gear identical to longline fishing gear (a horizontal main line with numerous gangions and baited hooks) set in segments < 1nm in length, requires no observer coverage or special permit beyond a State of Hawaii Commercial Marine License (CML, available for $50) and is not subject to seasonal closures (NOAA, www.nmfs.noaa.gov/pr/pdfs/fish-eries/hi_shortline.pdf, Itano 2004). Shortline and longline methods are often used on a single vessel and for the remainder of this paper the two terms are used interchangeably. Vessel participation at Cross Seamount has declined since the peak in

1996 with around 20 vessels working in the area (currently ~5-7 vessels), but recently concerns have been voiced about destructive fishery practices at Cross Seamount and vessel owners have complained about too many boats fishing in the area and not as many fish (Itano 1998, Pers. obs). There is additional concern for the sustainability of the pomfret fishery at Cross Seamount as little is known about the residency and habitat ecology of this potentially isolated population. Residence time (the amount of time a fish spends at a particular location prior to moving away, being captured, or preyed on) is an important metric for calculating maximum sustainable yield of a fishery, can be used to estimate the rate of removal of individuals from a population and is particularly important to consider for isolated populations (such as those on seamounts).

Studying seamount-associated fishes

Acoustic tagging and tracking studies can provide detailed vertical and horizontal movement data and quantify residency. It is relatively inexpensive and can be done aboard small vessels requiring only deployment and retrieval to collect year-long datasets illuminating the complexity and variability of fish behaviors (Weng et al. 2015). Few acoustic tagging studies of seamount associated or deep-sea teleosts been published (Priede 1990, Klimley 2003, Afonso 2012, Afonso et. al. 2014) primarily owing to the challenges of circumventing barotrauma related injury or mortality during capture (Gravel et al. 2008, Roach et al. 2011, Rogers 2011, Parker et al. 2006), and the challenges of working in deep water and offshore environments. However, severity of barotrauma in some deep-water species can be minimized, providing new insights into seamount fish ecology through acoustic tagging studies (Parrish 1993, Afonso 2012, Afonso et. al. 2014).

Using acoustic tracking this study investigated the feeding ecology and residence of a seamount associated fish by observing fine-scale movements and dependency of individuals on the seamount habitat at multiple time scales. Of particular interest was whether the fish were relying on one or more mechanism of trophic subsidy for feeding and whether they had a high dependency on the seamount habitat. The objectives of this study were to 1) evaluate the feasibility of tagging and tracking a seamount-associated teleost using acoustic telemetry 2) characterize three dimensional movements and habitat use of a valuable commercial fish at a seamount to determine if behavior is consistent with any mechanisms of trophic subsidy and 3) determine the level of residency of *Eumegistus illustris* at a seamount to investigate both the vulnerability of the population to the fishery and evaluate potential adult connectivity with other islands and seamounts.

Materials and methods

Study species

Eumegistus illustris (**Fig 2),** also known as the Lustrous pomfret or 'monchong' in Hawaii, is a commercially important pomfret commonly caught in Hawaii longline and bottomfish fisheries at depths of 270-620m around pinnacles and seamounts with summits shallower than ~450m (Mead 1972; Chave 1994). They range throughout the Main Hawaiian Islands and nearby Johnston Atoll (Ralston 1986, Weng *pers. comm.*) but degree of connectivity between the islands is unknown. This species is targeted as well as being caught incidentally by commercial longline boats at Cross Seamount (Itano 2004). *E. illustris* feed on micronekton such as myctophids, followed by squid, shrimp and crabs (Prut'ko 1985, Parin & Prut'ko 1985, Okamoto 1985). Pelagic juveniles settle to the benthos as adults (Mead 1973) suggesting isolated populations do not receive significant immigration of adults. However, adults are occasionally landed by longliners in pelagic waters implying movement between isolated habitats is possible.

Figure 2: Eumegistus illustris, the Lustrus pomfet (known as monchong in Hawaii)
A mesopelagic predator of Cross Seamount and deep slopes, *E. illustris* is a commercially important species often targeted and landed by Hawaiian fishermen.

Study site

Cross Seamount, the shallowest of 13 seamounts known as the Geologist Seamounts, is located approximately 290 km SSW of Honolulu, Hawaii, at 18° 43' N, 158° 170' W. It is the only guyot in the group, rising from ~4,000m depth to a plateau-like summit having a diameter of about 7km comprised of rocky outcroppings and sandy deposits (**Figs 3A and 3B**). The summit, a smooth ovate dome, shoals to a depth of 335m (Grigg 1987, Grigg 2002). Fishermen have reported periods of high current over 2 knots for weeks and over a knot for months (Geer, K pers. comm.) but currents have also been observed to change at time scales of under an hour (Domokos 2007). Cross Seamount is the only seamount within the Hawaii EEZ that supports a year round shortline fishery for bigeye tuna and *E. illustris* (Itano 1998).

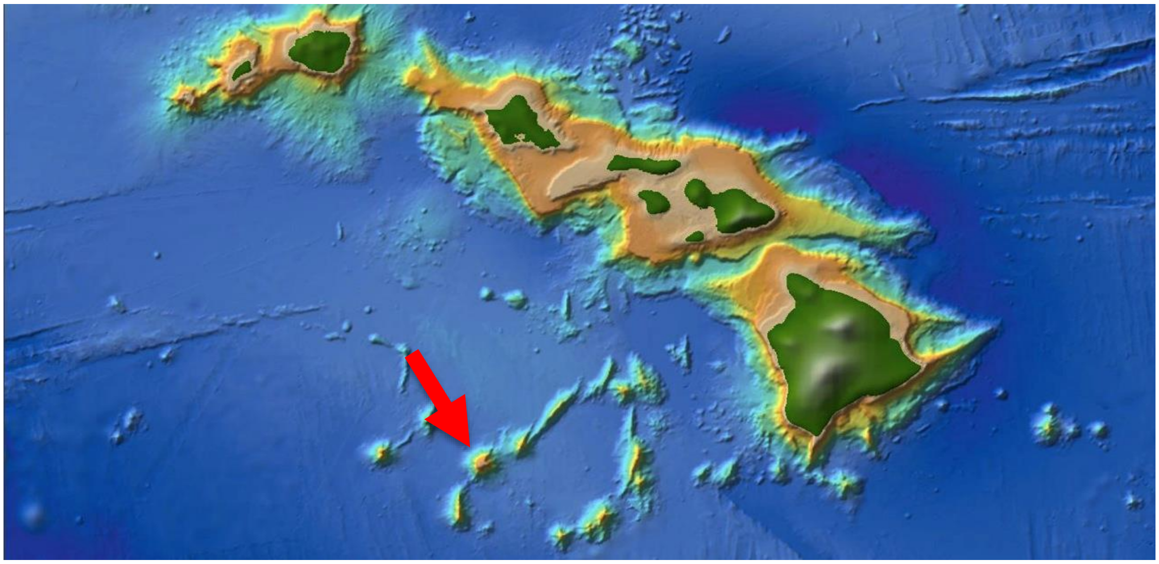

Figure 3A: Cross Seamount in relation to the Main Hawaiian Islands
(Source: Hawaii Mapping Research Group, SOEST, University of Hawaii)

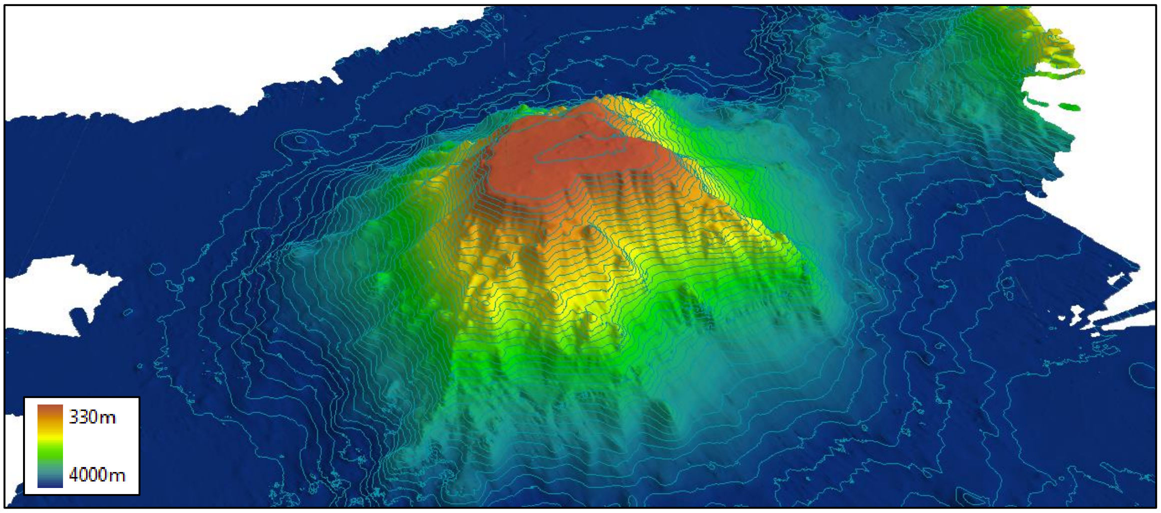

Figure 3B: Three dimensional rendering of Cross Seamount
(Source: Hawaii Mapping Research Group, SOEST, University of Hawaii)

Capture, tagging & tracking

I caught and tagged *E. illustris* during five trips to Cross Seamount aboard commercial longline vessels April 2010 to May 2012. Pelagic shortline and longline gear was set above the seamount at night and hauled in over multiple hours. Captured fish were placed dorsal side down in a padded cradle and irrigated by placing a hose in the fish's mouth and pumping water over the gills. As fish were brought to the surface air within their gas bladders expanded and in order to reduce injurious effects of barotrauma I vented fish with a hypodermic needle. I then inserted an internal acoustic tag into the peritoneal cavity via an abdominal incision, sutured it closed and tagged each fish with an external 'spaghetti' tag so they could be identified if recaptured. The best way to reduce barotrauma related mortality is to rapidly re-pressurize the fish as soon as possible (Parker et. al 2006) so I released fish on a weighted dropshot, quickly sinking them beyond the upper 100 meters of the water column. The entire tagging procedure typically took less than 5 minutes per fish. For the purpose of analysis, the fish tagged each year were considered a cohort. Therefore, cohort 1 was tagged in 2010, cohort 2 tagged in 2011 and cohort 3 was tagged in 2012.

I tagged 67 fish with 69 kHz acoustic transmitter tags (V13P-1x and V16P-4x) used in conjunction with VR2W acoustic receivers (Vemco, Nova Scotia Canada). These "V13" tags, rated to 200m depth and restricted to a maximum depth reading of 311 meters, emitted time and depth records every 60 seconds on average over an estimated 171-181 day battery life and were used with all 3 cohorts. “V16” tags, used only with cohort 3, were rated to 680m depth and transmitted every 90 seconds on average over an estimated 972-day battery life. I also tagged 18 individuals with LAT 1500 archival tags (Lotek Wireless, Ontario Canada) that collected depth at 5-minute intervals independent of the acoustic receivers and could be downloaded if recovered from a recaptured fish.

I placed an array of 5 to 10 acoustic receivers on the seamount summit at depths of 356-414m (**Fig 4**), which were mated with acoustic releases for remote retrieval (LRT, Sonardyne, United Kingdom). I used low vertical profile (< 4m) moorings with floats below the receiver to minimize entanglement with longline gear. Receivers had an estimated 500m detection range (Scherrer et al., unpublished). To compare horizontal movements of the fish between cohorts with different receiver arrangements, I binned stations into regions for analysis. Regions were divided by natural breaks in the acoustic array and were labeled North, East, Southwest and Middle.

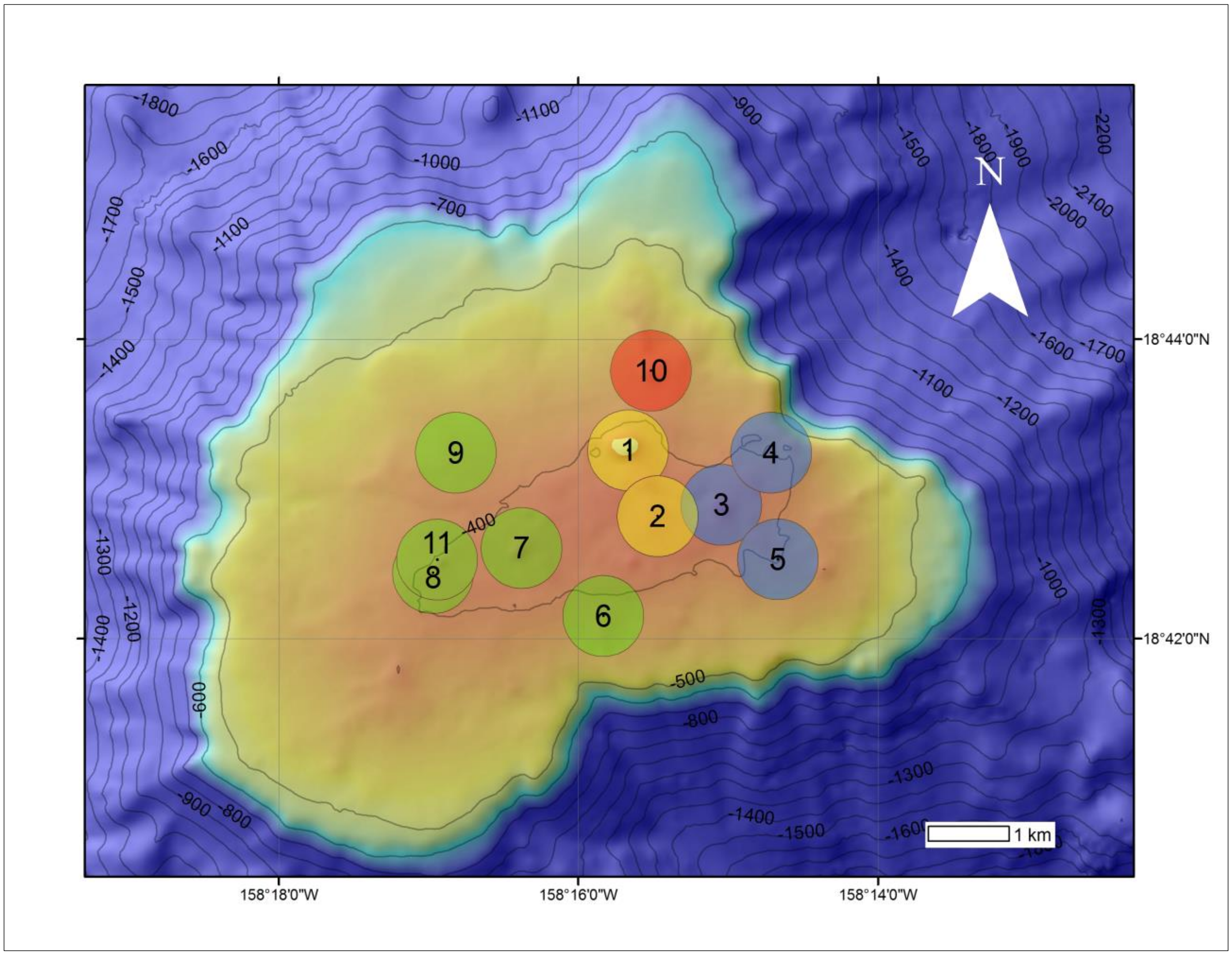

Figure 4: Map of Cross Seamount
Location and 500 meter detection radius of acoustic receivers on Cross Seamount. Green = southwest, yellow = middle, red = north, blue = east. The 2010 cohort had stations 1-4 and 6-10, 2012 cohort had stations1-7 and 10 and the 2013 cohort had stations 1, 4, 10 and 11.

Analytical approach

Analysis

I used tagging data to examine fish movement in the context of feeding ecology by comparing horizontal and vertical movements to micronekton distributions. Acoustic receivers recorded date, time, depth and tag identification number and archival tags recorded date, time and depth. Time is presented in Hawaii-Aleutian Standard Time (HAST). Analysis was done using JMP®, Version 12 SAS Institute Inc., Cary, NC, 1989-2007. Sunrise, sunset and nautical twilight times were based on forecasts by the Astronomical Applications Department at the US Naval Observatory in Washington, DC (aa.usno.navy.mil/data) for N18° 43’ W158° 16’. On average twilight began 50 minutes prior to sunrise and ended 50 minutes after sunset. Prior to analysis, spurious detections caused by transmitter code collisions (Heupel 2006) were removed, defined here as single detections within a 24-hour period. To ensure an equivalent influence of each fish on summary statistics regardless of the number of days recorded, mean values were calculated by first averaging data among individuals and then averaging between fish in the analysis unless stated otherwise. I used ANOVA or Welch's ANOVA to compare mean values between groups for equal and unequal variances respectively (Welch 1951). If distributions were non-normal a Wilcoxon rank sums nonparametric test was used instead. I used Levene's test to test for equal variance and a Shapiro-Wilk W to test if data was normally distributed when the sample size was small (Levene 1960). For normally distributed data I made multiple comparisons using a Tukey-Kramer honest significant difference (HSD) test that controls for type I error ($\alpha=0.05$). If I could not transform the data into a normal distribution I made multiple comparisons by the nonparametric Steel-Dwass method, similarly controlling for type I error (Hsu 1996). In addition to cited literature, observations of micronekton dynamics at Cross Seamount were collected by Reka Domokos aboard the NOAA ship *Oscar Elton Sette* and documented in reports by ASTWG, JIMAR and WPFMC from 2007-2009. These observations were compared to the movements of *E. illustris* at Cross Seamount to elucidate their feeding ecology.

Quality control

Detections recording depth errors, predation of tagged fish, dead fish and descent of fish directly after tagging were removed from analysis along with fish with insufficient detections (<200 detections or <24 hours, Appendix A).

Range testing

In order to assess the distance at which tags can be detected, I placed an acoustic V13-1x 30 meters above the substrate at Cross Seamount ~500m away from station 10 and ~630 meters from station 1 for 264 days. The tag transmitted a tag identification code every 20 minutes on average. The reference tag detection efficiency was presented as total detection rate (TDR = total # detections/estimated maximum detections possible) and hourly detection rate (HDR = # detections received per hour of 24-hour day/estimated maximum detections possible per hour of 24-hour day). I used a students t-test to compare average HDR between night, twilight and day.

Detection rate of fish

Part of determining the effectiveness of acoustic coverage involves understanding how the detection rate varies with environmental conditions, acoustic array design and fish behavior. To determine if the acoustic array coverage was sufficient for following *E. illustris* daily movements I calculated total detection rate (TDR) as: (# detections)/(estimated # total transmissions), with an estimated 1,440 transmissions per day. V16 tags broadcast an average of 960 transmissions per day and were normalized to 1,440 transmissions per day for this analysis. To see if the number of acoustic receivers used affected the detection rate of fish at the seamount I used a t-test assuming equal variance to compare TDR between groups cohorts 1-2 combined (8-9 receivers) and cohort 3 (4 receivers), first testing the distributions for normality and unequal variance. To ensure an effective tagging study it is important to identify biases that may affect detecting the fish. I calculated periodic detection rates (PDR) for night, twilight and daytime time periods for each day a fish was detected at the seamount as: (# detections per period)/(estimated # total transmissions per period). I compared average day, twilight and night PDR for individuals using a Tukey-Kramer HSD test. I also pooled mean detection rates for each fish and used a Wilcoxon rank sums test and a post hoc Steel-Dwass test to compare between average day, twilight and night PDR for all fish. To understand how detection ability changes with fish depth I calculated hourly detection rates (HDR) for all V16 tagged fish by first averaging depth or number of detections for each hour each fish was present on the array and then again by hour of the day producing twenty-four mean depth values for five fish. An ordinary least squares regression and an ANOVA was used to test the relationship between mean depth and HDR.

Seamount habitat utilization

I used two indices of horizontal movement around the seamount to understand habitat use and identify critical habitat area: ‘occupancy’ (unit = time), and ‘activity’ (unit = region). Time between consecutive detections less than 6 hours apart within a single region were summed for each day and each night. The region with the greatest value for each day or night was considered the area of occupancy during that period. Consecutive detections overlapping the day/night boundary (sunrise or sunset) were split at the boundary. For example if 2 detections occurred in the SW region at 1800 and 1845 and sunset was at 1830 then 30 minutes would be assigned to 'day' and 15 minutes to 'night' in that region. Time was allocated to day or night as follows: day = sunrise to sunset, night = sunset to sunrise (following day). Daily and nightly activity was calculated as the mean number of regions visited each day and each night a fish was detected on the seamount. I used a matched pairs t-test to compare length of occupancy between night and day and average activity level between night and day.

Vertical behavior

I examined *E. illustris* depth profiles to identify DVM behavior, position relative to micronekton and to distinguish between seamount-associated and pelagic behavior. I calculated daytime and twilight depth statistics only for V16 tagged fish, which have sufficient depth ratings. I designated 'behavioral state' of the V16 tagged fish as 'benthic' or 'pelagic' based on proximity of fish to the seamount (Afonso *et al.* 2014). If the fish was within 2 standard deviations of the mean depth of the seamount within the 500m detection radius of the receiver it was considered to be in a 'benthic' behavioral state and if it was shallower is was considered in a 'pelagic' behavioral state. The ratio of behavioral states for day, twilight and night was calculated for each fish, $\log_{10}$ transformed to normalize the distribution and compared using a Tukey-Kramer Honest Significant Difference (HSD).

Understanding how *E. illustris* benefit from the seamount topography can be elucidated by observing them away from the seamount, which is possible for fish tagged with both acoustic and archival tags that left the seamount. A Welch's unequal variance t-test was used to determine if there was a difference in depth between seamount associated and non-seamount associated states.

Seamount residency

I used the duration and frequency of detections to consider the importance of the seamount habitat at multiple time scales. Residence time at the seamount was used to understand how long *E. illustris* remain at Cross Seamount and was calculated as days from the first detection to last detection or recapture date. Recapture dates were estimated as the middle of the fishing trip on which the fish was caught with trips around 2 weeks long. 'Residency indices' are a measure of the proportion of days a fish is detected at a region or on the array as a whole (see Afonso et al. 2012) and were calculated from the date of the first detection to the last detection (e.g. a fish detected on four separate days over a duration of ten days would have a residency index of 0.40). Residency indices between regions had a non-normal distribution and were compared using the Steel-Dwass method. A Wilcoxon rank sums nonparametric test was run between cohorts 1 and 2 combined and cohort 3 in each region and all regions together to see if residency indices were significantly different between the first two cohorts and cohort 3. To determine how often and how long fish were absent from the array gaps between detections were calculated and binned in the following groups (in hours): <3, 3-6, 6-12, 12-24, > 24.

To help understand the connectivity of *E. illustris* with other seamount or shelf habitats I calculated typical swimming speeds of fish using the minimum time between detections of a fish at pairs of stations >2.5 km apart (to reduce the influence of unknown detection distances, estimated at 500m). The locations of detections were conservatively estimated at the edge of the 500m detection radius for each station so distance swam between two stations is 1km less than the distance between those stations and ranged 1.66-3.13 km. Transit times beyond 2 hours were unlikely to be directed movements and not used for analysis.

Results

Receiver recovery

Not all receivers were recovered as a result of longline entanglement or the failure of certain acoustic releases. I lost station 5 for cohort 1, stations 8 and 9 for cohort 2 and cohort 3, which only had five stations deployed, lost station 6. Analysis for cohorts 1-3 used 9, 8 and 4 receivers respectively (**Fig 4**).

Quality control

Forty-one fish were dropped from further analysis. Epipelagic predators ate three fish shortly after release, 13 fish did not have sufficient detections for analysis and 25 fish were never detected. About 20% of total depth records were removed from 12 fish due to tag depth sensor errors resulting from tags exceeding the maximum rated depth. Twelve fish had detections trimmed after presumed death indicated by a sudden end in vertical and horizontal movements followed by disappearance. Detections of descent during post-tagging release were also removed from analysis.

Range testing

The reference tag had high short-term variability (**Fig 5A**) but relatively low long-term variability (**Fig 5B**) revealing daily trends in detection rate. The total detection rate (TDR) dropped off steeply between ~500m (75%) and ~630m (<0.1%). At 500m the reference tag had 0-4 detections per hour with a daily average of 2.25 (*SD* = 0.92). HDR had a bimodal distribution with lows at 0400-0500 and 1600-1700 (*M* = 2.08, *SD* = 0.93, *HDR* =69%) and highs at 2200-2300 (*M* = 2.45, *SD* = 0.82, *HDR* = 82%) and 0800-0900 (*M* = 2.31, *SD* = 0.91, *HDR* = 77%). A small but significant difference was observed in HDR between day and night (HDR_{day} = 73%, HDR_{night} = 77%, p = 0.028) but twilight was not significantly different from either night or day (HDR_{twi} = 74%).

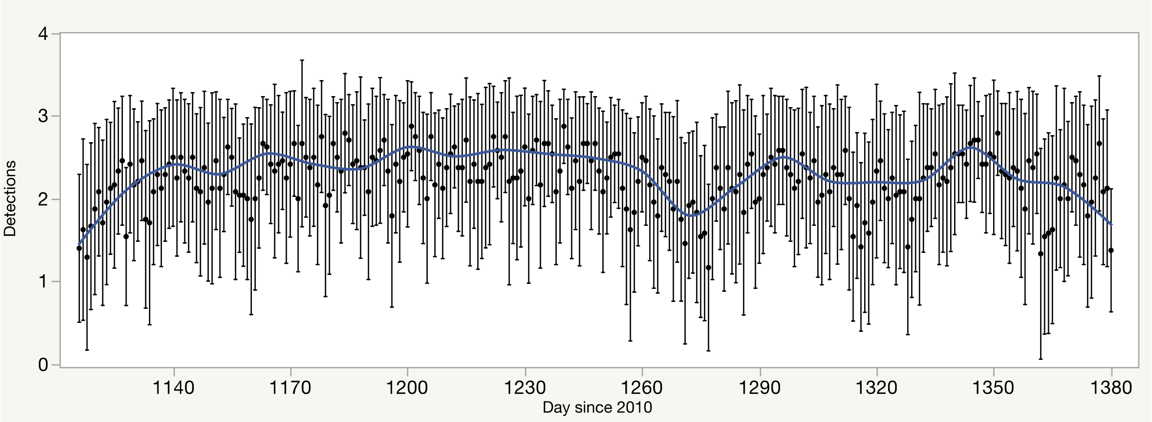

Figure 5A: Detection rate over life of reference tag
Mean hourly detection rate and standard deviation with spline. Three detections per hour is considered 100% detection rate.

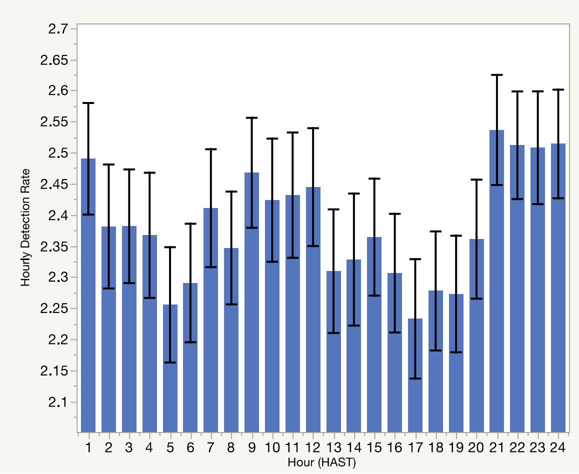

Figure 5B: Detection rate over 24 hour day
Mean hourly detection rate over 24 day. Error bars represents 95% confidence interval. Three detections per hour is considered 100% detection rate.

Ability to track fish

Twenty-six fish, identified hereafter as the 'detection group,' had 1,019-54,291 detections over 7-371 days (**Table 1**). Most fish (81%) were detected all days between their first and last detection but five were not detected for 2-26 days (*M* = 15.4). Twelve fish were first detected the same day as they were tagged, 13 fish were first detected 1-5 (*M* = 1.9) days after tagging and one fish was first detected 90 days after release **(Figure 6).**

Table 1: Detection summary
Detection summary of 26 fish tagged and tracked. FL = fork length, Detection = total number of detections after quality control, % vertical data = the % of detections with depth positions not removed due to errors, Last detection = last day an acoustic detection was received from the fish, Range of days detected = number of days fish was at liberty (Last detection – Date tagged + 1), # days detected = number of days the fish was detected on the acoustic array.

Fish ID	FL	Detections	% vertial data	Date tagged	Last detection	Range of days detected	# days detected
164	71	9,171	43%	9/5/10	10/30/10	55	55
173	64	9,077	14%	4/6/11	5/14/11	39	39
175	61	4,575	100%	4/6/11	4/26/11	20	20
177	63	8,672	24%	4/6/11	5/7/11	31	31
178	68	1,539	100%	4/7/11	4/21/11	15	8
179	65	1,019	100%	4/7/11	4/13/11	7	7
180	65	9,281	53%	4/7/11	5/22/11	46	46
182	70	7,483	100%	4/7/11	5/14/11	38	38
184	68	54,291	100%	4/9/10	10/7/10	177	177
185	71	6,194	19%	4/9/10	6/11/10	64	64
191	67	9,377	63%	4/5/11	6/11/11	68	59
192	53	4,148	100%	4/5/11	4/30/11	26	26
193	67	7,153	0%	4/5/11	5/22/11	48	48
194	76	11,664	58%	4/6/11	5/23/11	47	47
195	65	6,325	100%	4/5/11	5/6/11	32	32
237	59	11,293	100%	10/4/12	4/7/13	181	155
239	70	8,088	100%	10/4/12	12/1/12	58	58
248	69	2,741	33%	10/5/12	11/12/12	39	39
249	68	2,757	23%	10/5/12	11/12/12	39	39
252	71	2,950	78%	10/5/12	11/16/12	42	42
255	67	3,527	0%	10/5/12	1/8/13	95	95
400	70	5,245	100%	9/30/12	11/16/12	47	47

401	**68**	**1,905**	**100%**	**9/30/12**	**10/28/12**	**28**	**28**
403	**57**	**26,083**	**100%**	**10/2/12**	**10/11/13**	**371**	**346**
410	**68**	**7,510**	**100%**	**10/2/12**	**11/30/12**	**58**	**58**
413	**70**	**45,430**	**100%**	**10/4/12**	**10/10/13**	**285**	**283**

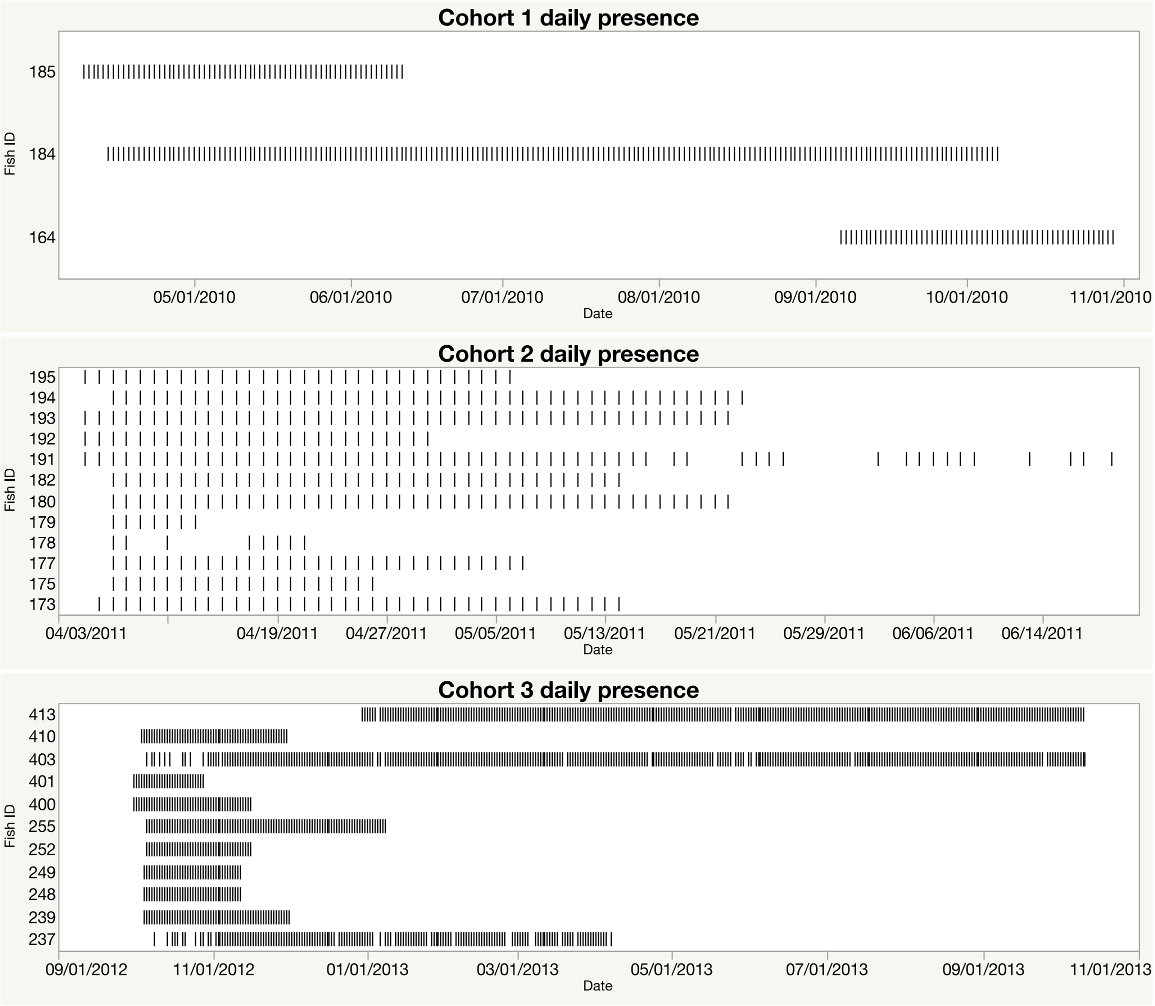

Figure 6: Residency of individuals at the seamount
Black bar indicates the fish was present at one or more receivers over a 24-hour day (HAST).

Total detection rate (TDR) was 2.6-21.3% (*M* = 11.0%, *SD* = 5.0%). Fish averaged 1.9-19.7 (*M* = 10.6, *SD* = 5.4, *TDR* = 17.3%) detections per hour at night, 0.2-8.3 (*M* = 3.8, *SD* = 2.0, *TDR* = 6.3%) during the day and 1.5-27.2 (*M* = 6.9, *SD* = 5.9, *TDR* = 11.5%) at twilight. Mean TDR for cohorts 1 and 2 (*M* = 13.1%, *SD* = 4.3%) with 9 and 8 receivers respectively was significantly greater than for cohort 3 (*M* = 7.9%, *SD* = 4.4%) with 4 receivers.

Twenty-one fish from the detection group had the highest periodic detection rate at night, three fish (413, 178, 184) had the highest PDR at twilight and two fish (400, 401) had the highest PDR during the day. Five of the twenty-one fish (178, 179, 248, 401, 410) showed greater PDR during the night then the day and seven fish also showed significantly greater detection rate during twilight than daytime. Overall median fish PDR was not equal between time of day (X^2= 25.231, *DF* =1, $p < 0.0001$) with night > twilight > day ($p < 0.05$, **S1 Fig, F1 Table).**

For v16 tagged fish mean depth explained 40% of the variation of hourly detection rate ($R^2 = 0.40$, $F(1, 118) = 79.85$, $p < 0.0001$, **Figure 7**) suggesting behavior is a major influence on detection ability.

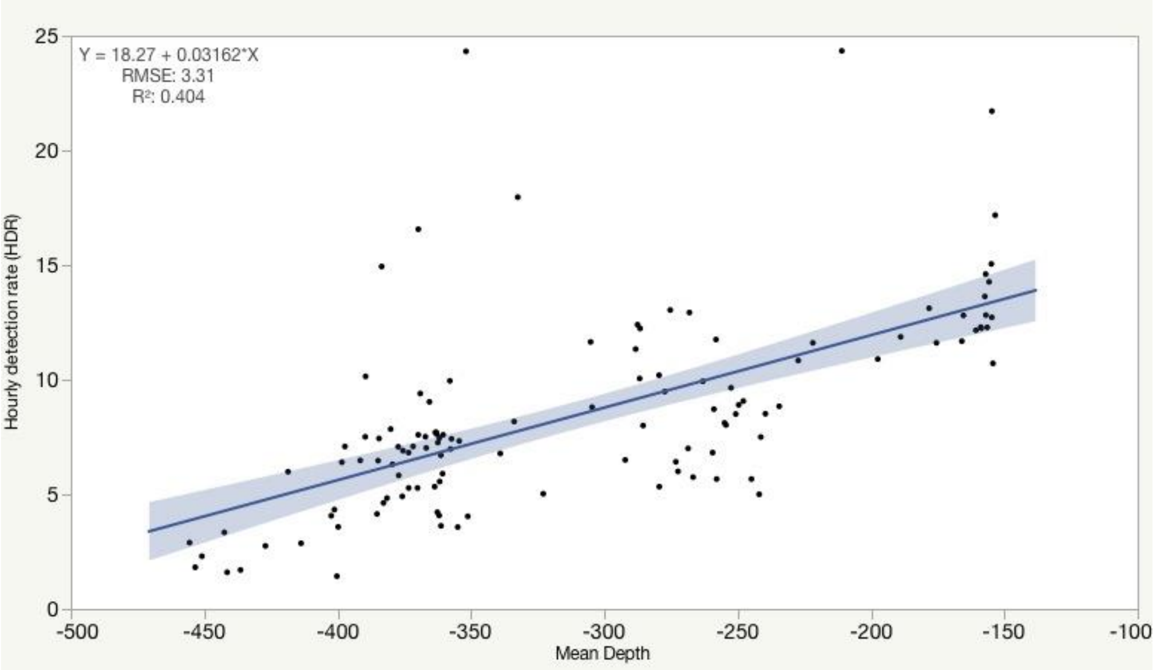

Figure 7: Detection rate vs depth
Ordinary least squares regression of mean depth of each hour of the day and mean number of detection for each v16 tagged fish (fish 400, 401, 403, 410, 413). Blue shading represents 95% confidence interval.

Recapture rate of fish in commercial fishery

At least 4 (15.4%) of the detection group were recaptured by commercial longliners 285-744 days after release, two of which had archival tags (**Table S1**). Nine individuals within the detection group showed eventual signs of death (ceasing of vertical and horizontal movements followed by disappearance), and another was eaten by a predator. Assuming these 10 fish were not candidates for recapture the proportion of recaptured fish at Cross Seamount increases to

25%. The 12 other fish that were not recaptured all eventually ceased being detected on the array within 8 to 95 days.

Seamount habitat utilization

Average occupancy was significantly longer during the day than during the night (n = 26, *t*(25) = -3.15, *p* = 0.0142). During the day occupancy was 0.37 to 9.62 hours (*M* = 5.96, *SE* = 0.61) and 2.50 to 8.57 hours at night (*M* = 4.74, *SE* = 0.52). During the day all but five fish showed occupancy at the middle region more than any of the other regions for 49-97% of days tracked (**Fig 8***)*. Averaged over all fish 69% of occupancy was in the middle region, followed by North and Southwest (13%, 12% respectively) and East (6%). At night all but five fish showed occupancy at the middle region more than any of the other regions for 43-95% of nights tracked. All had occupancy in the middle region and all but one had occupancy in the East region. Averaged over all fish, 56.5% of occupancy was in the middle region, followed by East (25.5%), Southwest (12%) and North (6%). Occupancy in the East region is sparse during the day but it is heavily utilized at night (mean 6% and 26% respectively).

Fish tended to move between regions more regularly at night than during the day. Average nightly activity was significantly greater than average daily activity (n = 26, *t*(25) = -7.32, *p* < 0.0001). During each of the days detected, fish visited 1-4 regions with daily activity of 1.16-2.52 (*M* = 1.94) regions and nightly activity of 1.5-3.16 (*M* = 2.48) regions (**Fig 9**). Daily activity indicated that the fish are still moving significant distances when close to the seamount. All but two fish (185 & 248) had greater daily activity than nightly activity.

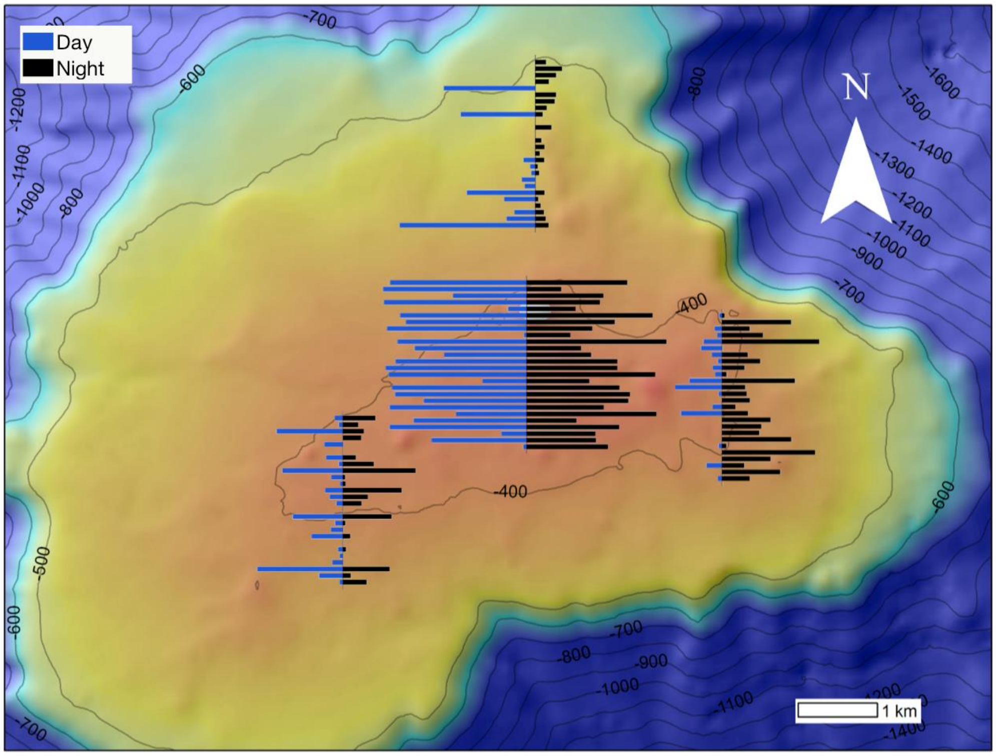

Figure 8: Location of occupancy
Location of occupancy as a proportion of all days or all nights for each fish. Sum of blue bars is one for each fish, and sum of black bars is one for each fish. Each row represents a single fish (see figure 8 for fish identification numbers) with numbers increasing from top to bottom. Plot locations correspond to the four regions of the seamount (from left to right): Southwest, middle, north and east.

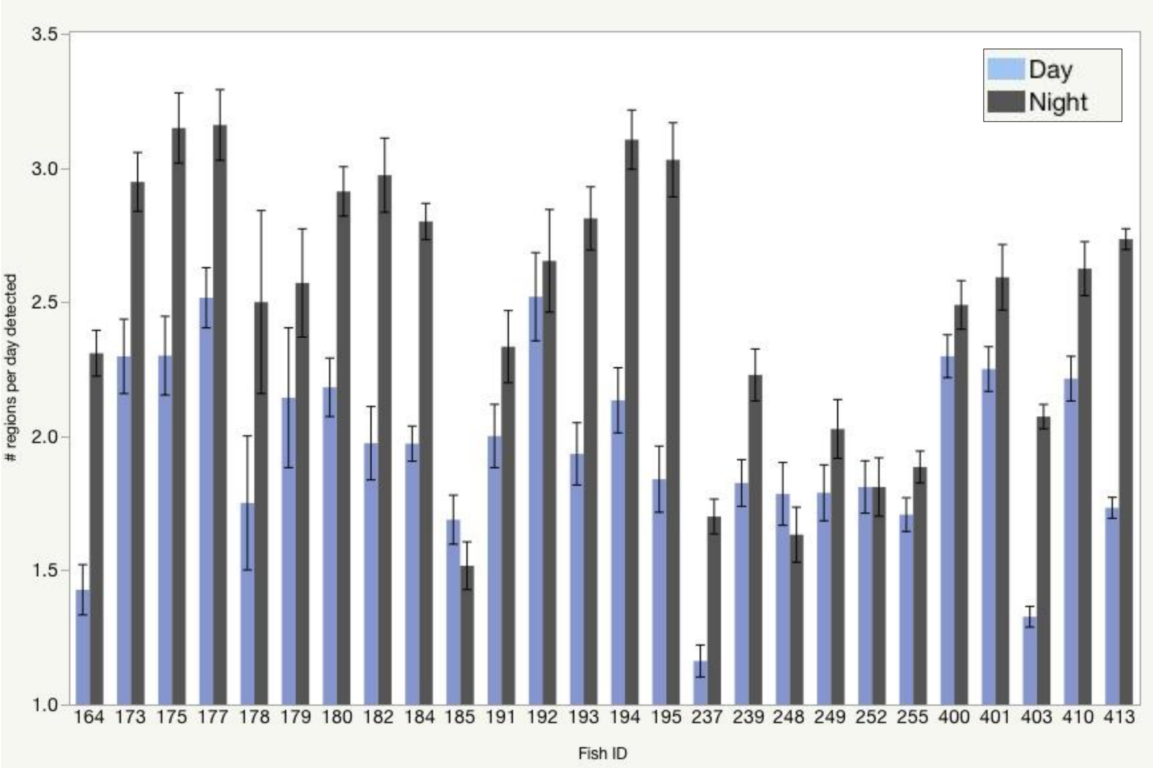

Figure 9: Daily and nightly activity
Number of regions visited per day each fish was detected at Cross Seamount. Error bars are standard error.

Vertical behavior

E. illustris behavioral state was strongly pelagic at night becoming less pelagic during the day. The five V16 tagged fish had a pelagic:benthic detection ratio of 2.3 (*SE* = 1.1) during the day, 19.6 (*SE* = 24.4) at twilight and 1070 (*SE* = 865) at night. Log_{10} transformed pelagic:benthic ratios were significantly greater at night than during the day ($p = 0.024$) but not between night and twilight or twilight and daytime ($p > 0.05$) (**Fig 10)**. Daytime behavioral state was about half benthic, but may have a greater benthic component then measured since detection ability decreases as the fish swims deeper.

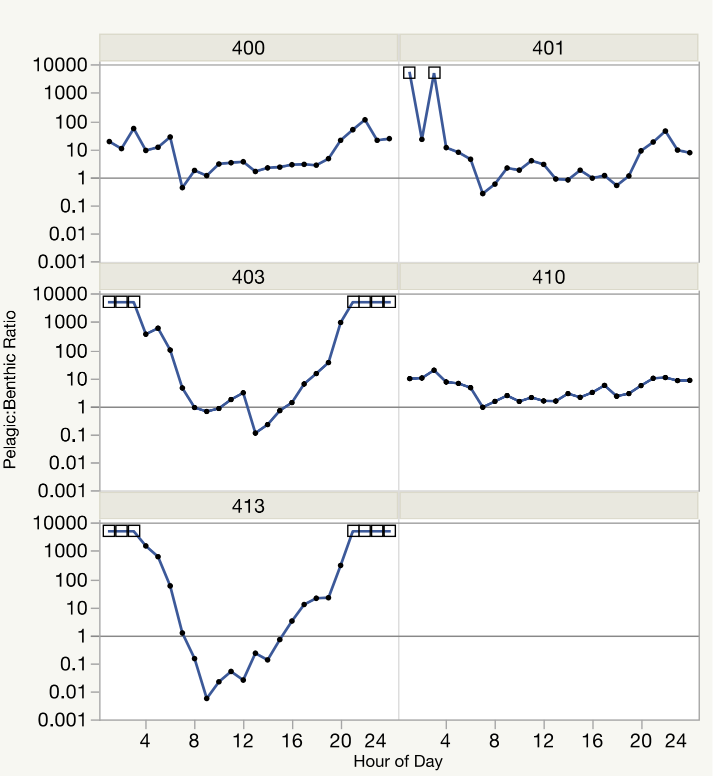

Figure 10: Pelagic to benthic ratio
Average pelagic:benthic behavioral state ratio for five fish tagged with v16 transmitters through a 24-hour day. Values above one indicate a predominantly pelagic behavioral state and values below one indicate a predominantly benthic behavioral state. Squares indicate hours that do not contain any benthic detections and fish can be considered to be in a completely pelagic behavioral state.

All *E. illustris* with depth records displayed consistent vertical migratory behavior ascending to shallower depths around dusk and remaining primarily in the shallower water until the approach of dawn (**Fig 11, Table S2**). Five fish (178, 184, 237, 403, 413) had night depth profiles considerably shallower than the others with mean nighttime depths ranging 157-189m depth compared to the other 19 individuals with mean nighttime depths 240-299m. Minimum recorded depths of most fish were around 200m but five individuals made excursions to ~100m and one individual went as shallow as 63m. Nighttime vertical movements above 311m were observed with V13 tagged fish but depth sensors bottomed out for 0-84.1% (*M* = 25.1%) of detections. Vertical depth ranges encompassed the majority of the water column (~57-80%) between the surface and maximum fish depths undergoing about half their vertical depth range (~40-60%) on a daily basis (**Fig 12)**.

Daytime depths of V16 tagged fish ranged 260-487m with average depths of 361-380m.

Twilight depths ranged 107-429m with average depths of 254-341m. Maximum depths were 454-487m, minimum depths 95-194m, daily average depth ranges 179-297m total depth ranges were 260-384m. Depth of fish did not appear to be affected by temperature or oxygen concentration (**Fig S3)**. As a group, daytime mean depth was slightly shallower than the mean bottom depth around each station (11-50 meters above the mean bottom depth, **Fig 13**) as well as for individual fish at most stations (although 3 fish had average depths 5-7m deeper than the mean depth at station 11).

Two archival-tagged fish (237 and 413) were recaptured with records covering 150-278 days. Immediately after tagging fish 413 left the acoustic array for 90 days before returning to the seamount. When away from the seamount fish 413 had deeper average nighttime ($p = 0.045$) and daytime ($p < 0.0001$) depths than at the seamount (**Fig 11).** Both fish had consistent nightly vertical migrations regardless of association with the seamount.

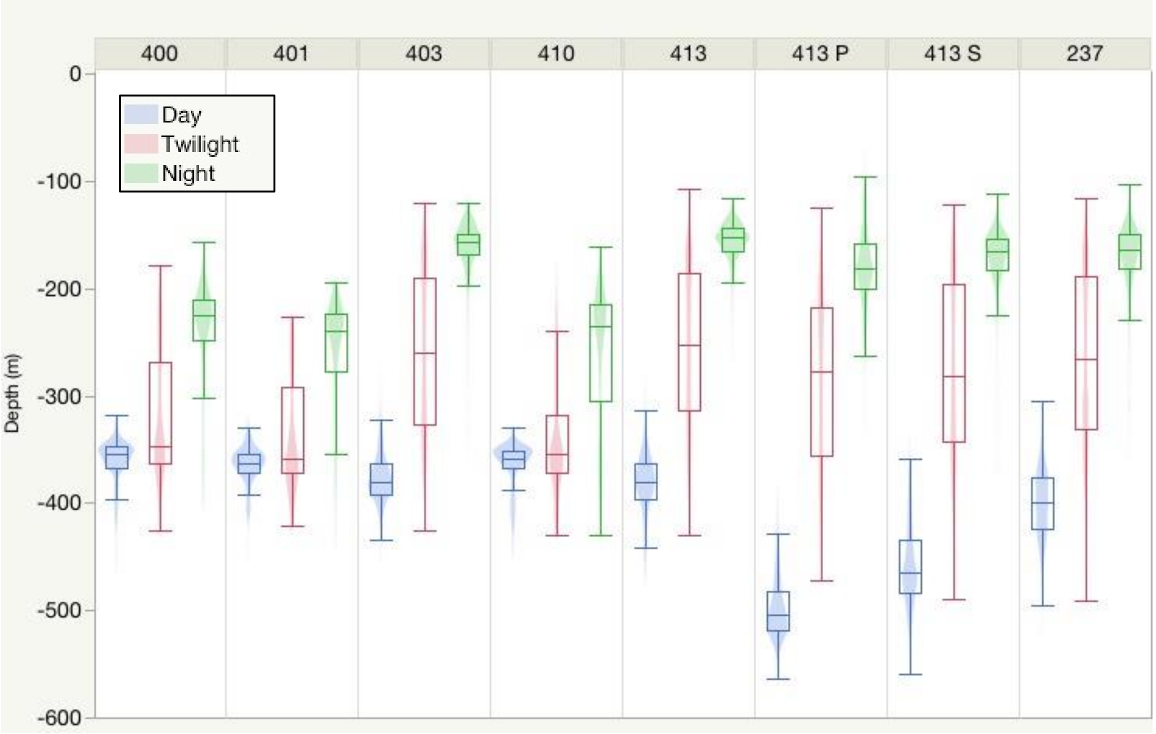

Figure 11: Depth ranges of v16 and archival tagged fish
Depth profiles of four fish tagged with v16 transmitters, one fish tagged with an archival tag (237) and one fish (413) tagged with both. Fish 413 is displayed as acoustic data only (413), archival data when away from the seamount (413 P) and archival data while present at the seamount (413 S). Acoustic data from fish 237 is limited to a depth of 311m and is not displayed here. Boxplots indicate 1st and 3rd quartiles, median, 1st quartile - 1.5 x (interquartile range), 3rd quartile + 1.5 x (interquartile range). Shaded regions indicate relative density of detections. Blue = day, red = twilight, green = night.

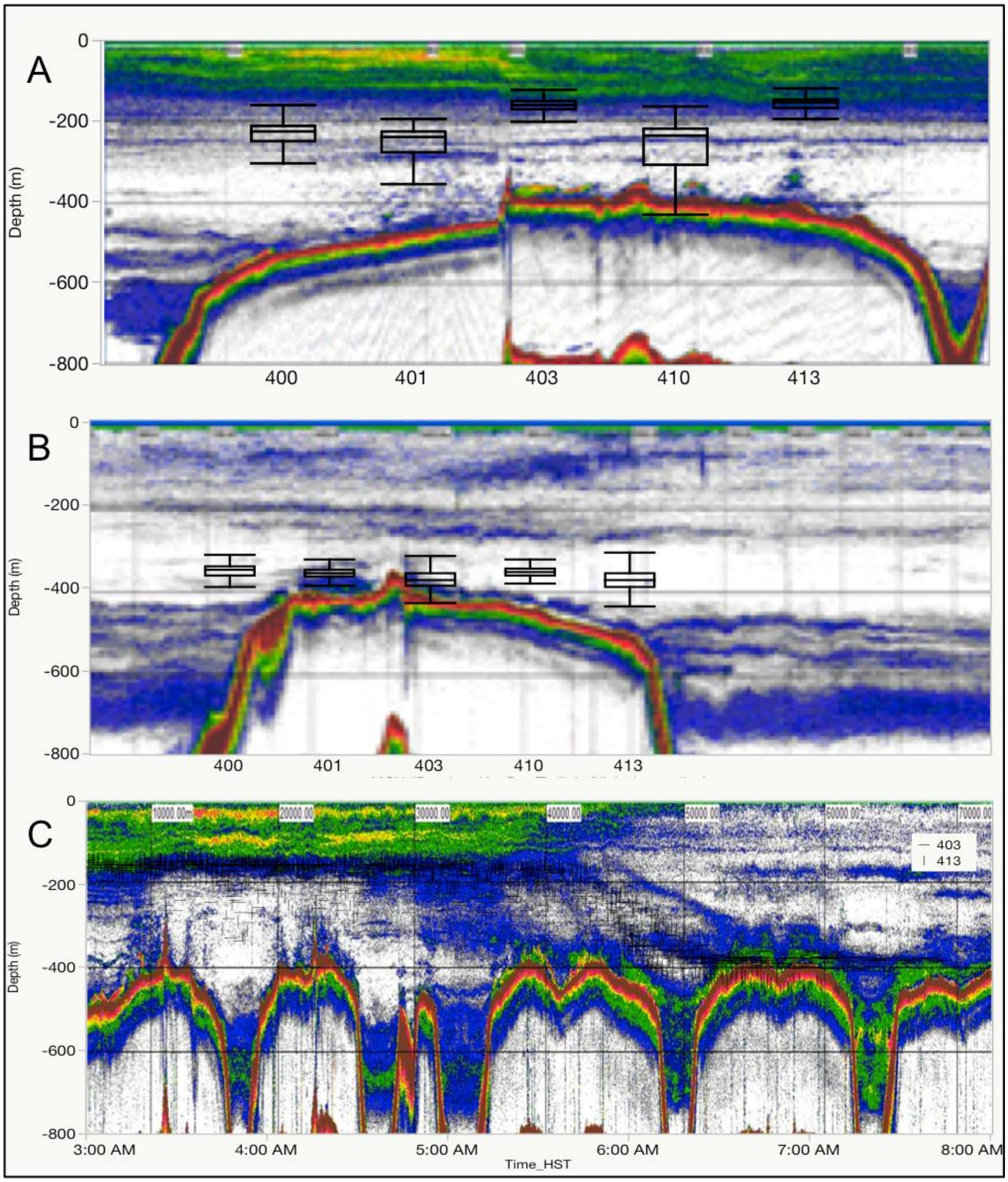

Figure 12: *E. illustris* and micronekton vertical distribution
Boxplots indicate the vertical distribution of five V16 tagged fish during the A) night B) day. C) Black markers indicate position of fish at dawn in April 2013 overlapped with backscatter plots from April 2007. All backscatter plots from Domokos (2007). Boxplots indicate 1st and 3rd quartiles, median, 1st quartile - 1.5 x (interquartile range), 3rd quartile + 1.5 x (interquartile range).

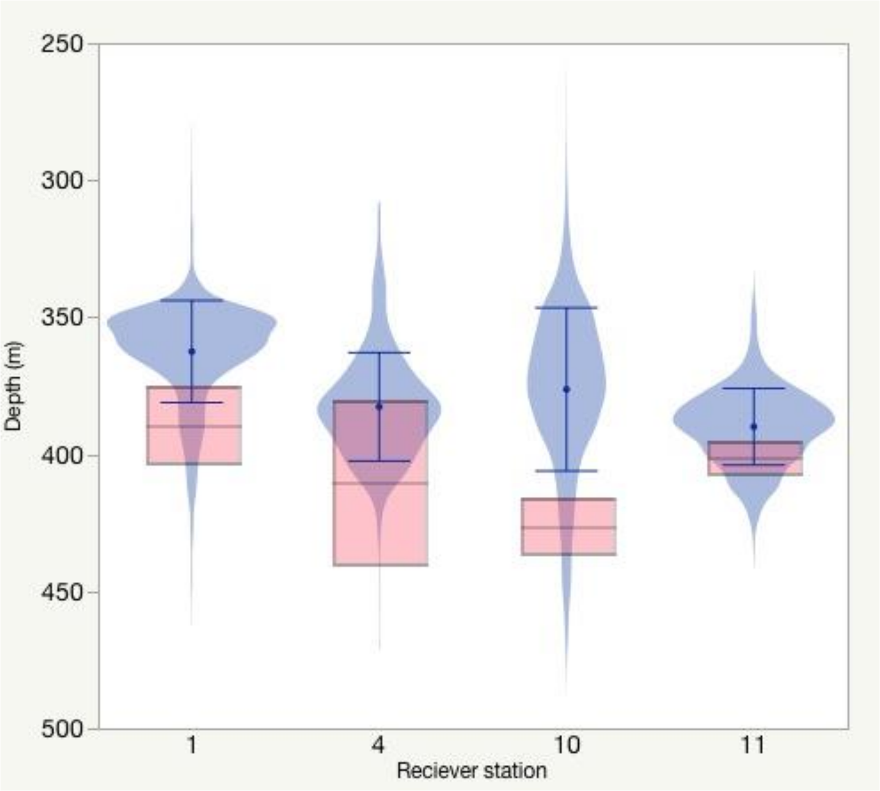

Figure 13: Bottom depth vs. daytime fish depth
The red box indicates the mean and standard deviation of bottom depth within the 500m detection radius of each receiver station. The blue point and error bars denote the mean depth and standard deviation of all detections pooled from the five V16 tagged fish at each receiver station. Blue shading indicates the depth distribution of detections throughout the depth range of the fish for each station.

Residency time on seamount

The residence time for *E. illustris* at Cross Seamount was 7-741 days (*median* = 46.5, *M* = 103, *SD* = 162). Only half of the fish were present beyond 45 days from the first detection (**Fig 14**).

E. illustris tend to stay within the acoustic array on a daily basis once they are initially detected. During their time tracked, 21 of the fish did not leave the array for over 24 hours and three fish did not leave for more than 12 hours (**Fig 15)**. Of the five fish that did leave for over 24 hours, the time away from the array during the 2-36 departures accounted for 1.6-60.3% (*M* = 29.4%) of their time detected with the longest departure of 156 hours (6.5 days, fish 191).

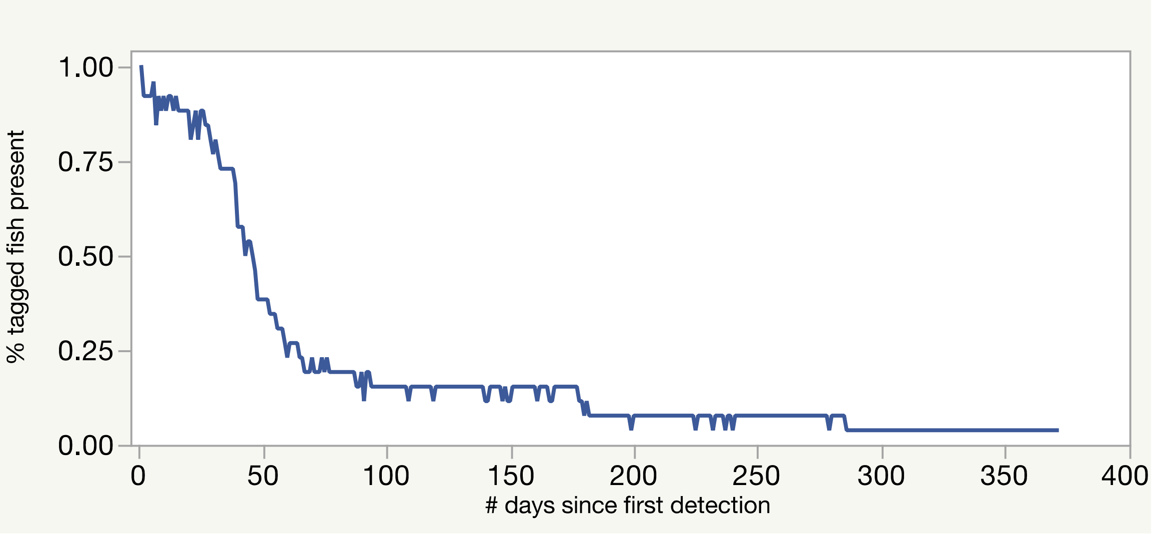

Figure 14: Proportion fish present
Proportion of total number of fish detected in the acoustic array each day since initial detection.

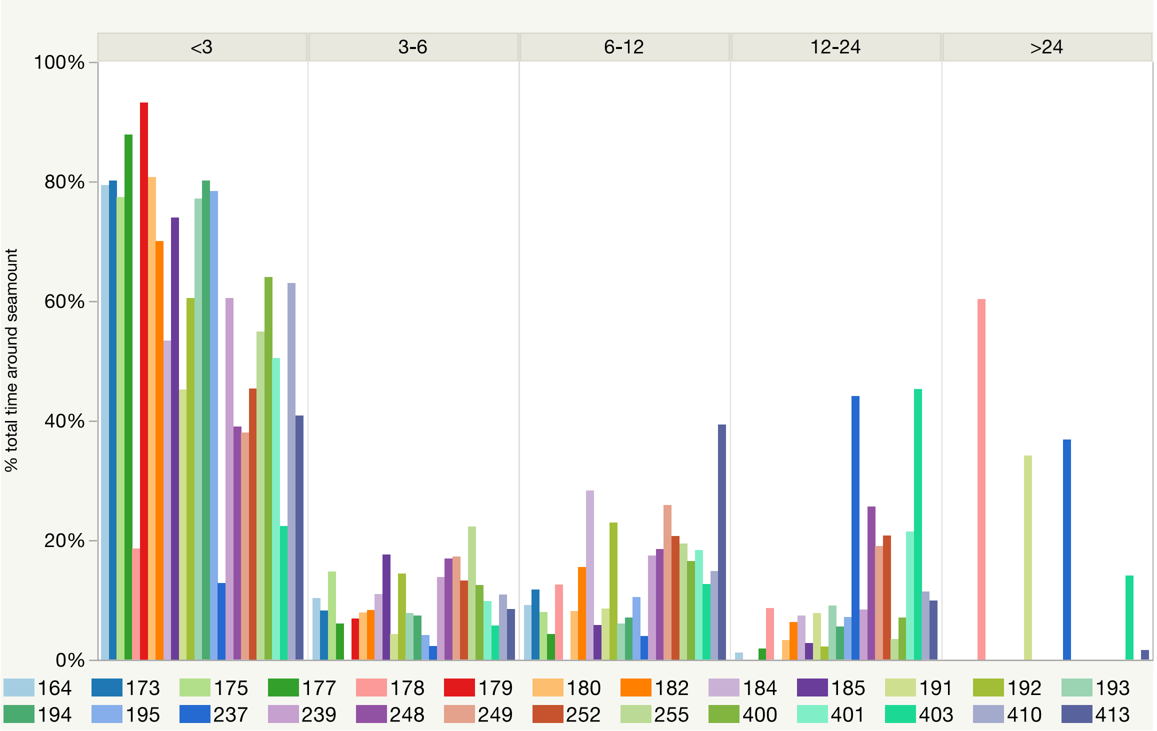

Figure 15: Gaps per day
Proportion of time between first and last detection spent within detection gaps of <3 hours, 3-6 hours, 6-12 hours, 12-24 hours and >24 hours.

Mean residency indices ranged from 0.47 at the southwest region to 0.92 at (**Fig 16**) the middle region; an area only about 1.8-3.7% of the 42km^2 Cross Seamount summit. On average there was a 97% chance each a fish was detected each day on the array (between the first and last detections). Overall, median residency indices of regions were significantly different from one another ($p < 0.05$, **F2 Table**) except between north and east regions ($Z = -1.50172$, $p = 0.56130$) and between the middle region and all regions combined ($Z = 2.51862$, $p = 0.0865$). At the southwest region cohort 3 had median residency indices significantly lower (*Med* = 0.57, $X^2 = 3.2171$, $DF = 1$, $p = 0.0729$) than cohorts 1 and 2 (*Med* = 0.31). Median residency indices were not significantly different between cohorts ($p > 0.05$) at any other region or at all regions combined.

Directed long-distance movements of fish between pairs of stations had maximum sustained speeds of 1.6 to 3.3 km/hr (**S3 Table)**. This assumes straight-line movements and greater actual speeds could be expected. A third (33%) of all directed movement concluded between 0620-0840 shortly after sunrise (**S4 Fig**).

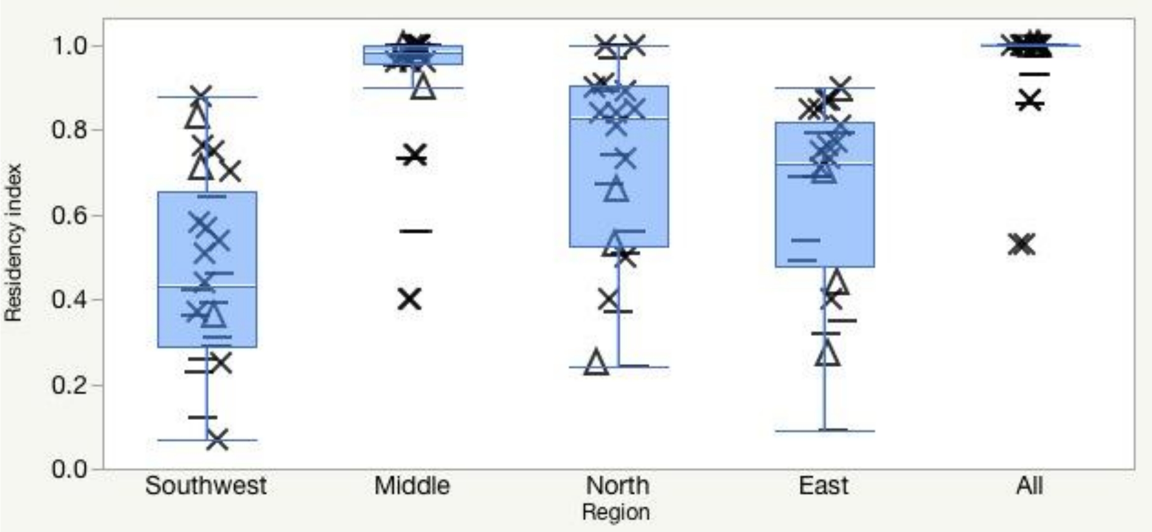

Figure 16: Residency indices by region
Cohorts are designated by markers: triangle = cohort 1, X = cohort 2, dash = cohort 3. Boxplots indicate 1st and 3rd quartiles, median, 1st quartile - 1.5 x (interquartile range), 3rd quartile + 1.5 x (interquartile range).

Discussion

Feasibility of tracking seamount fishes

The main challenges in this study related to mitigating injuries to fish during capture while working aboard commercial longliners within the limitations of fishing success at a remote seamount. Working at a heavily fished site lowered receiver recovery rates but enabled high recapture rates and allowed for the recovery of archival tags and provided extended records of depth and duration for two fish. Profuse movements of fish, a large acoustic detection range around receivers and appropriate acoustic receiver placement on the seamount allowed me to record movements of a mesopelagic seamount associated fish at a scale not often observed in acoustic studies.

Barotrauma related mortality can sufficiently be reduced to conduct a viable deep-water teleosts tagging study to observe individual fine scale movements but remains the greatest challenge for tagging deep seamount-associated fish and is especially problematic in the context of residence. Capture and tagging can be stressful for fish and mortality can be common in tagging studies, especially one targeting deep-water physoclistous fish (Parrish 1993, Grimes 1983, Gravel 2008, Roach 2011). Tagging blackspot seabream (*Pagellus bogaraveo*) at Condor seamount in the Azores archipelago Afonso et al. (2012) experienced similar rate of undetected or under-detected fish as this study (57% and 61% respectively) and similarly attributed it primarily to mortality without ignoring the possibility of emigration. In tagging studies properly identifying injured fish and selecting healthy individuals to tag is important but choice can be limited by fishing success, especially on seamounts, which are often very remote and difficult to access. In fish exposed to sudden ascent from depth barotrauma related injuries can lead to mortality, both at the surface and after re-pressurization upon release (Parrish 1993, Gravel et al. 2008, Roach et al. 2011). Exophthalmia, or the bulging of the eyes, due to rapid pressure change can stretch the optic nerves and muscles of the eye and cause temporary vision impairment (Rogers 2011). Without proper selection of appropriate tagging subjects synergistic effects of injury and stress from capture, rapid temperature change, handling and surgery may lead to mortality.

Fishing method and gear type may influence fish rate of ascent, a key determinant of barotrauma. *E. illustris* rapidly brought to the surface on bottomfish gear showed unrecoverable barotrauma related injuries upon surfacing (Pers. obs.) but longline capture reduced the effects of barotrauma by catching them at shallower nighttime depths and gradually bringing them to the surface. Even so, dissections of longline caught *E. illustris* showed that some fish exhibiting few signs of barotrauma had ruptured swim bladders, thus releasing expanding air but damaging their buoyancy mechanism. Parker et al. (2006) found that most rockfish would recover after rupturing their swim bladder from a 3 atmosphere change in pressure, but *E. illustris* likely underwent 10-20 atmosphere changes in pressure (resulting in ~3-6 times the gas expansion of the study) and differences in species specific response to pressure changes were significant, even within the same genus.

Other capture techniques of deep-water teleosts have been documented to mitigate pressure related injuries to fish. One possible method for further increasing survivability of deep-water fish is subsurface tagging in order to avoid the greatest rate of pressure change although it is operationally more difficult (Parrish 1993). Afonso et al. (2012 & 2014) used another successful capture technique, catching blackspot seabream with handlines as they swam at least 50m above the 200m summit (rather than conspecifics found along deeper slopes) and slowly hauled them up at a rate of about 0.2m/second. While they were able to use this method successfully it could present problems in areas of high shark depredation.

The ability of receivers to detect acoustic tags can be highly variable by habitat and through time (Simpfendorfer 2007, How & Lestang 2012). How & Lestang (2012) tested V13 and V16 acoustic receivers in shallow reef environments and observed primarily sigmoid shape detection rate curves with distance. At most locations they had a consistent detection rate of reference tags of 65-85% out to ~300-400m after which there was a sudden drop in detection rate. The reference tag average detection rate (75%) and distance from the receiver (500m) in this study suggest that a similar shape of detection dissipation was experienced with an extended range compared to the shallower waters of the study. Simpfendorfer et al. (2007) discuss a wide variety of disruptions that can modify acoustic tag detection rates including tag collisions, biological, physical or anthropogenic generated noise, the orientation and anchorage of the receivers, the behavior of the tagged animal and environmental incongruities such as stratification. At Cross Seamount changes in detection rate prior to crepuscular hours (possibly due to acoustic blockage by layers of DVM organisms) were relatively small, especially considering the high detection variability and did not affect results. In this study changes in detection rate were primarily driven by fish behavior (e.g. proximity of the fish to the substrate) with transmissions physically blocked by topography or acoustically inhibited by noise from benthic fauna. Archival records revealed that some individuals had depth ranges deeper than acoustic tags recorded, but that may be limited to a few individuals that preferred deeper daytime habitat. For these reasons daytime movement analysis should be taken with caution and treated as minimum estimates when compared with shallower nighttime behavior until range testing can be conducted at multiple depths to integrate potential biases.

Nonetheless, acoustic coverage of fish was exceptional and highlights the benefits of tracking fish at isolated seamounts. *E. illustris* spent ample time on the summit within the acoustic array and had relatively few detection gaps giving a detailed look into vertical and horizontal movements of individuals. Afonso et al. (2012) had similar average detection rates ~10% (total detections/estimated maximum detections of 720 per day) for their detection group but experienced much higher variability between individuals (*M = 9.0%, SD = 13.6%)*. However, this detection rate is uncommonly high and many tracking studies have frequent and extended gaps in detections and provide only snapshots of fish behavior or intermittent position estimates (Meyer et al 2007, Weng 2013).

Our low profile mooring design could have exacerbated the effect of decreasing detection rate with increasing fish depth but was necessary to avoid longline gear entanglement. Studies conducted in areas without longline fishing should place receivers higher in the water column with the hydrophone facing down in order to get better coverage of fish close to the bottom and position floats far above the receiver to allow detection of the fish high in the water column. As demonstrated here, only a few receivers interspersed over a seamount may be necessary to return high-resolution behavior. If the goal is to only detect presence a single receiver may be sufficient for highly mobile species like *E. Illustris* and return similar residency index measurements as an entire array. Ideal placement on seamounts would be at the highest point in order to reduce blockage by terrain.

Foraging behavior and ecological advantages to living on a seamount

Sometimes suggested as an energy saving bioenergetics strategy (e.g. Sims et al. 2006), DVM has repeatedly been observed as way for predatory fish to increase prey interceptions.

Strong shallower nighttime depth preference for *E. illustris* was highlighted, with individual variability, as all fish maintained nightly vertical migrations with crepuscular transitory periods. Comfort & Weng (2015) used satellite popup tags to measure speed and velocity of bluntnose sixgill sharks (*Hexanchus griseus*) during daily migrations between 600-300m and likewise suggested these sharks foraged more actively in shallow waters at night than the day but feeding was unlikely during crepuscular hours as they moved between habitats. Using sonar and trawl surveys Gauthier & Rose (2002) followed daily vertical migrations of deep-water Atlantic redfishes (*Sebastes spp.*) and found that the fish movements coincided closely with their micronektonic prey and stomach content analysis indicated nightly feeding. Furthermore, they noted that daytime schooling near the seafloor may be a form of 'energetic refuge' removing the fish from currents and allowing them to remain in one place with little effort—highlighting a potentially important strategy of vertical migrators at an isolated seamount. Clearly following micronekton distributions through the water column *E. illustris* may descend to maintain contact with the seamount through the day possibly feeding opportunistically as they continue to move around the seamount to a lesser extent.

E. illustris morphology (muscular bodies, scales, well ossified skeletons, swim bladder presence) and food preference (myctophids, squid and shrimp) is indicative of DVM behavior (Salvanes & Kristoffersen 2001), which proves to be fundamental to the daily movements on and off the seamount. Unlike other mechanisms of trophic focusing DVM behavior is not seamount specific (Sims et al. 2006, Polovina et al. 2008, Comfort 2015, Sassa 2002, Gauthier & Rose 2002) and for *E. illustris* it appears to be equally as important in the pelagic as at Cross Seamount. However, transformed by local micronekton dynamics and protruding bathymetry at Cross Seamount, DVM behavior can exploit seamount specific habitats and micronekton distributions. The critical importance of DVM to *E. illustris* is apparent by the consistency at which it occurs—with V16 and archival tags recording migrations every night. The only other study to date documenting individual seamount fish diel vertical migrations by Afonso et al. (2014) also observed nightly migrations with depths matching micronekton distributions to a certain degree.

Fish feeding on the mesopelagic boundary community could be expected to ascend with the migrating scattering layer at night, remaining over the seamount to feed on unique or enhanced micronekton layers, perhaps continuing to feed on resident micronekton over the summit after descent. Seamount associated micronekton can have strong swimming ability, keeping them from getting swept off the seamount at night while in the water column (Domokos 2008, Wilson & Bohlert 2004, Wilson 1992). *E. illustris* is a strong swimmer capable of capturing fast moving species and were observed nightly at depths overlapping the mesopelagic boundary communities in the water column. DeForest & Drazen (2009) found fewer pelagic species over the summit of Cross Seamount compared to adjacent pelagic waters. Seamount associated species were also caught, but with potentially greater swimming ability some could have avoided the 140 m^2 Cobb trawl used in the study. *E. illustris* nighttime positions over Cross Seamount match with micronekton abundances greater than the pelagic (shallower than 200m) or at depths completely absent of micronekton in the pelagic (200-400m, Domokos 2007-2009). At the Condor seamount summit (depth ~200m), Porteiro (2013) observed high zooplanktivorous biomass that could significantly contribute to the diet of resident benthopelagic fish. Bioacoustic surveys at Cross Seamount suggest similar increased local forage availability (Domokos 2007-2009) and daytime horizontal movements point to *E. illustris* benefitting from these greater daytime foraging opportunities. Individuals not observed on the summit or expressing frequent movement between regions were primarily located on the deeper slopes of the seamount partially out of acoustic range, but according to the limited archival data from fish 413, are likely undergoing continuous movement, possibly feeding on the enhanced DSL. The high residency indices of fish at the seamount indicate that *E. illustris* is strongly benthic associated, often maintaining close association with topographic features and likely an important component of the seamount food web, deriving a large portion of it's diet from seamount-associated micronekton.

Cross Seamount may be an ideal location for fish to take advantage of a feed-rest lifestyle; resting protected from currents by the seamount topography and only needing to make short excursions to feed on nearby prey (Genin 2004). Strong currents and anticyclonic water movement on Cross Seamount likely entrain zooplankton (Domokos 2009) and create a stable flux of food to deep-water corals and inactive fish (Grigg 2002). Thick micronekton aggregations surround the seamount at deep scattering layer depths as well as over the top of the summit, providing foraging opportunities near to resting places. Feed-rest behavior should be common on the edges of shelves and seamounts where much pelagic prey first contacts the bottom (Brodeur 2001, Genin 2004) and at Cross Seamount the thick DSL below 500m could provide continuous feeding opportunities for fish along the slope or individuals could rest along shallower edges of the plateau when DVM prey swims over the edge of the seamount during descent at dusk (Domokos 2008). However, most fish had occupancy predominantly at the center of the seamount. *E. illustris* may benefit from the occasional prey item carried past them in the currents over the top of the seamount or along the flanks in the deep scattering layer but it is clear that primary feeding behavior of this species at Cross Seamount is not feed-rest driven. At the scale of the acoustic network feed-rest behavior would appear as few horizontal movements between receivers and small vertical movements. Rather than continuous small scale movements indicative of feeding on a constant flux of impinging micronekton and zooplankton (Koslow 1997) the fish undergo large daily vertical migrations of hundreds of meters to search for their forage—sometimes covering a large area of the seamount summit in a single night. Horizontal and vertical movements decrease during the day but the fish are still actively moving between receivers, often in a pelagic behavioral state away from the protection of the seamount. These results align with Genin & Dower (2007) who propose that the horizontal flux of food to resting fish at moderate depth seamounts is likely a minor ration when compared with other prey consolidating mechanisms such as topographic blockage, presence of mesopelagic boundary community or feeding on micronekton layers during diel vertical migrations.

The depth, geomorphology and oceanographic characteristics at Cross Seamount make topographic blockage a potentially important feeding mechanism. Positioned between the DSL and SSL depths the expansive summit creates a considerable area for descending micronekton to avoid. Additionally, strong currents paired with weak to absent rotational flow in the upper 200m of the water column over the seamount where most of pelagic micronekton reside at night (Johnston et al. 2008, Domokos 2007), should renew the population of pelagic micronekton descending over Cross Seamount at dawn. Topographic blockage can occur across the entire extent of a seamount blocking descending DVM organisms, but is often most pronounced at the edges of the seamount (Fock et al. 2002a, Fock et al. 2002b, Genin 1988). In the early morning this process can greatly concentrate the availability of prey by at least 40 times what is found in the water column and provide benthopelagic fishes the greatest feeding opportunity of the day

(Isaacs & Schwartzlose 1965, Seki & Somerton 1994). Position of *E. illustris* on the seamount after dawn is variable with most preferring the middle region but certain individuals preferring the northern slope. At dawn all individuals descended and established a primarily benthic behavioral state, positioned to exploit the vertical compression of micronekton blocked by seamount topography. This indicates that topographic blockage supports daily energetic requirements of *E. illustris* but the relative importance is difficult to determine. The lack of synchronization of position on the seamount at the time of micronekton descent suggests that either the effect is widespread or feeding behavior is opportunistic and secondary to feeding in shallow waters at night.

At Cross Seamount increased forage appears to be available to *E. illustris* through multiple mechanisms of trophic subsidy and relative importance may vary between individuals. Daily vertical migrations position *E. illustris* to feed on pelagic and mesopelagic boundary community species and exploit trapped micronekton upon descent. A minority within the detection group had shallower nighttime depth preference and utilized a distinctive daytime habitat closer to the periphery of the summit and seamount slopes. Micronekton from the MCB have been seen via acoustic sounders over Cross Seamount swimming actively down and over the edges of the summit, even against prevailing current (Domokos 2008 & 2009) and certain individuals may have feeding strategies exploiting a micronekton accumulation along the slopes. Consequently, the relative importance of each mechanism is likely to vary between individuals.

Benthic habitat use and residence time

The average residence time of *E. illustris* at Cross Seamount was around 100 days but was highly variable between individuals and should be received with caution, as it is unclear how tagging affected survivorship or emigration. The high stress and potentially injurious capture and tagging process may have reduced survivability of certain individuals and it is unclear how much that drove the sharp decline in *E. illustris* residence around a month post-tagging. Tagging has been used to calculate residence time in shallow species (Holland & Grubbs 2007, Barnett 2012, Muir unpublished) but working with deep-water species presents unique challenges (Parrish 1993, Weng 2013). Residence time calculations from acoustic telemetry data are constrained to the battery life of the tags but can help identify post-tagging mortality (Afonso 2012) and predation events. Average residence times for bigeye tuna (*Thunnus obesus)* at Cross

Seamount were significantly longer when assessed using acoustic telemetry (Muir et al. unpublished) than previously published results using conventional tagging methods (Holland & Grubbs 2007). For deep-water fish with high post-release mortality like *E. illustris*, a combination of conventional and acoustic tagging can provide excellent insight of emigration and fishing mortality and help assess residence time. In this study fish recaptures extended residence time estimates beyond the acoustic records by 95-373 days. *E. illustris* are capable of moving into pelagic waters or to other benthic habitats and disappearance from the seamount could be attributed to emigration, fishing mortality or natural mortality. Afonso et al. (2012) modeled attrition rate from twelve acoustically tracked blackspot seabream at Condor seamount and estimated a 50% chance of detection of tagged fish after 278 days and the longest period they monitored a fish was 829 days. However, the mean residency index was only 25% compared to 97% at Cross Seamount. *E. illustris* had a more rapid attrition rate with half of fish still detected around 45 days post tagging, but some fish were resident for much longer periods of time with the four recaptured fish enjoying a time at liberty of ~285-741. These stretches at the seamount prior to capture with high daily presence and a feeding ecology dependent on the seamount habitat suggest fish often remain at Cross Seamount for years, potentially permanently.

However, emigration from the seamount to pelagic waters or distant benthic habitat cannot be discounted. Almost half (46%) of the detection group disappeared between 8-95 days without indications of predation or death and 25 individuals outside the detection group were never detected on the acoustic array and 14 had only a few detections before disappearing, possibly leaving post-tagging as fish 413 did. Unfortunately, chances of recapturing fish away from the concentrated fishing effort at Cross Seamount are low. Long gaps in detections, usually beginning at night, are indicative of pelagic forays and were an uncommon occurrence among most individuals. Intermittent pelagic feeding opportunities may present themselves making it favorable to move to pelagic waters. For example, a number of long disappearances from fish 403 and 237 coincide in late October 2012 and again in early January 2013 along with fish 413 and may represent times of good forage in pelagic waters away from the seamount.

The middle region of Cross Seamount consistently proved to be an important habitat for *E. illustris* especially during the day when most fish spent the majority of their time in the region. Fish were more likely to be detected in the middle region than any other region and the area had a similar residency index to all regions combined. Monitoring the shallowest area of a seamount has the advantage of reduced blockage from surrounding substrate and should be a preferred location for receiver placement in seamount studies. As well as containing the shallowest point of the seamount the middle region has a unique bathymetric feature. Surveys from an ROV and the Pisces IV submersible in 2000-2001 indicate that the geomorphology in this area consists of a large dome-like pinnacle with smooth ridges absent of precious corals *Gerardia* sp. and *Corallium* sp. which were abundant on another pinnacle closer to the edge of the summit and served as an aggregating point for the benthic shark *Echinorhinus cookei* (Grigg 2002, T. Kerby pers. comm.). Chave and Mundy (1994) noted that most benthic fish taxa observed at Cross Seamount occurred close to hard substrates with relatively high rugosity and *E. illustris* were associating with habitat surrounding the summit during the day.

Management implications

At Cross Seamount continuous high fishing pressure and widespread movements of *E. illustris* lead to high catchability. Longline vessels may each set 4-5 series of lines per day of up to 200 hooks, retrieving them after they drift across much of the seamount. Itano (2004) observed average *E. illustris* catch per 100 hooks at 1.4 when targeting bigeye tuna and 8.2 when targeting *E. illustris* but anecdotal reports from fishermen have claimed much higher yields in certain conditions. Copious daily movements of *E. illustris* and strong association with the seamount increase potential interactions with longlines. All fish remaining at the seamount over 100 days were eventually captured by longliners implying high fishing mortality for the population. In contrast, pelagic species targeted at Cross Seamount such as bigeye tuna are visitors to the seamount and therefore have a much lower catchability in this seamount fishery.

Prolonged fishing pressure can have profound effects on an area in regards to damaging the benthic habitat and fauna and may directly or indirectly threaten benthopelagic fish. Using video transects on the Condor Seamount Pham et al. (2013) observed a high abundance of litter, primarily fishing related, over the summit and slopes. At Cross Seamount submersible pilots have observed high instances of longline damage to benthic fauna including damage to gold corals (*Gerardia sp.)* and entangled cook sharks (*Echinorhinus cookei,* Terry Kerby pers. comm). In my experience many fishermen treated the area with disregard, including throwing all trash overboard and cutting lengthy segments of competing fishermen's baited longline free to sink to the bottom.

Confirming anecdotal reports, *E. illustris* are not confined to seamount habitat and can survive extended periods of time in completely pelagic waters, possibly transiting long distances to other benthic habitats. Cross seamount is the shallowest seamount in the region and the closest benthic habitat shallower than 600m is Penguin Banks ~240 km away. There have been numerous studies indicating that fish are able to navigate between seamounts from afar (Holland & Grubbs 2007, Klimely 1993). Dynamic and seasonal fish aggregations have often been observed over seamounts, with few details concerning individual movements between seamounts outside of aggregating periods (Morato 2007). Alfonsinos (*Beryx splendens*), a demersal seamount-associated fish undergo ontogenetic shifts in habitat utilization and age specific migrations between seamounts (Lehodey 1994, Lehodey 1997). Orange roughy (*Hoplostethus atlanticus*) are believed to migrate between seamounts in order to form spawning aggregations (White 2009). However, the one confirmed fish in the present study to leave the seamount may not have found suitable habitat as evidenced by its later return.

Videler and Wardle (1991) reviewed the swimming speeds of 27 fish species based on a variety of laboratory conditions noting that there could be significant variability among individuals as well as temperature, body size, and method the speed was measured. Sustained swimming speeds reported were greater than *E. illustris* for all species reviewed suggesting the measured speed is an underestimate. Using a conservative speed estimate of 2.0 km/hr, *E. illustris* could swim to Penguin Banks (~240 km) in 5 days (a shelf off of the west coast of Molokai Island in the Main Hawaiian Islands and an area where Hawaiian bottomfish fisherman regularly catch *E. illustris*). Likewise in the time fish 413 left the seamount it could have traveled over 4,000 km. These results demonstrate that *E. illustris* may transit through pelagic waters for extended distances and have the ability to move between seamounts as an adult. However, movements between seamounts are unlikely to occur in the Geologist Seamount chain since none of the other seamounts in this region shoal to the depth range of *E. illustris* (Okamoto 1982, Chave 1994).

In this study I used a novel method to interpret the feeding strategy of a mesopelagic seamount-associated predator that used diel vertical migrations to take advantage of multiple mechanisms of trophic subsidy. Furthermore, I was able to better understand the spatial ecology of a seamount-associated fish and discuss it in terms of connectivity and vulnerability. I also extended the working depth of published seamount-associated teleost acoustic studies and implemented an acoustic array design that obtained exceptional coverage over a seamount. The largest challenge encountered was implicit high post-release mortality, which affected the ability to accurately quantify residence and emigration. If capture and release methods can be improved to reduce barotrauma sufficiently acoustic tagging studies could become invaluable tools to study movements, habitat utilization and connectivity of deep seamount-associated fish. This information can be valuable to successful management of seamount fisheries in the face of commercial exploitation and can help create an ecosystem-based management approach to seamount fisheries.

Supplementary figures

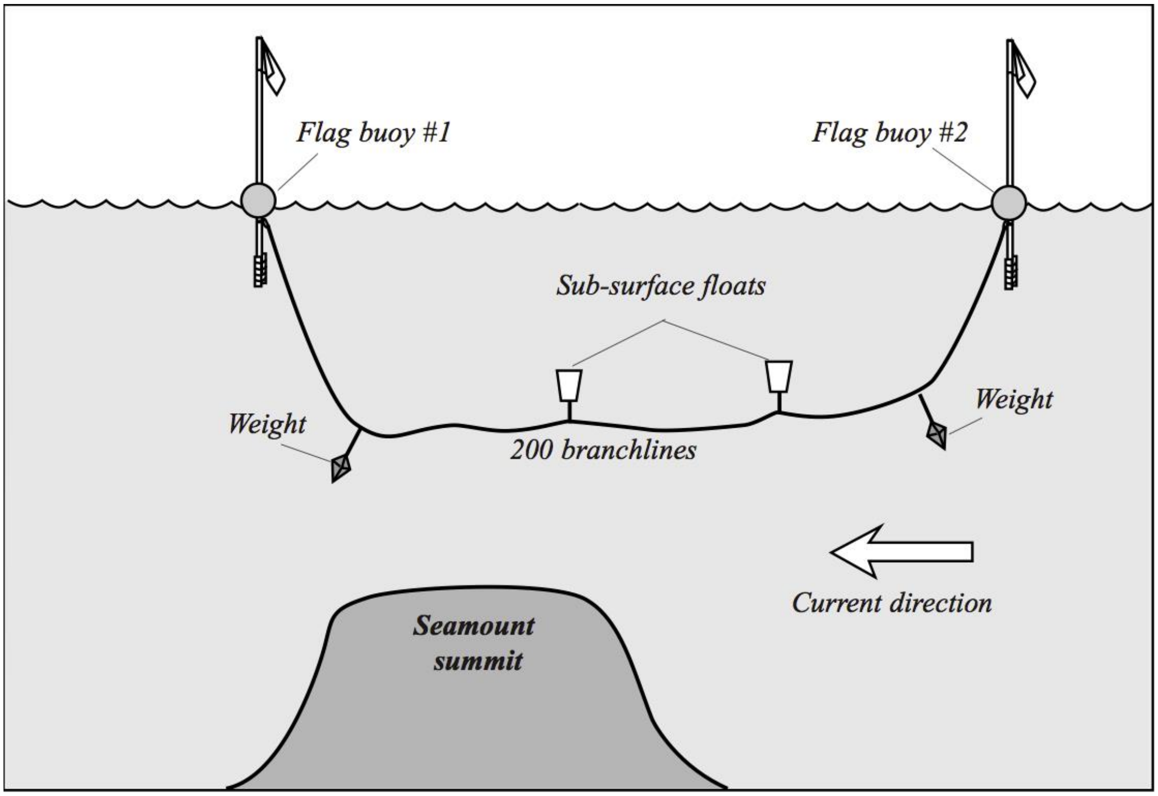

Figure S1: E. illustris 'shortline' gear setup (Beverly et. al. 2004)
'Shortlines' are set up-current of the targeted area and drift over the seamount during the night to target *E. illustris* used at Cross Seamount

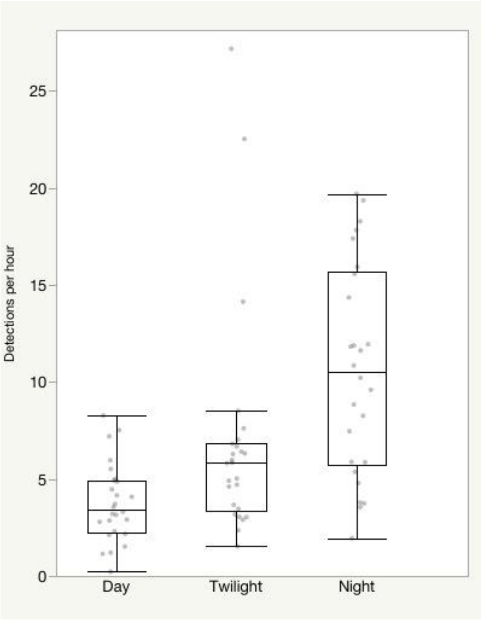

Figure S2: Detection rate
Boxplot of detection rate values from each fish for day, night and twilight. Detection rate has been normalized between V13 and V16 tags. Each mark indicates the detection rate for a single fish.

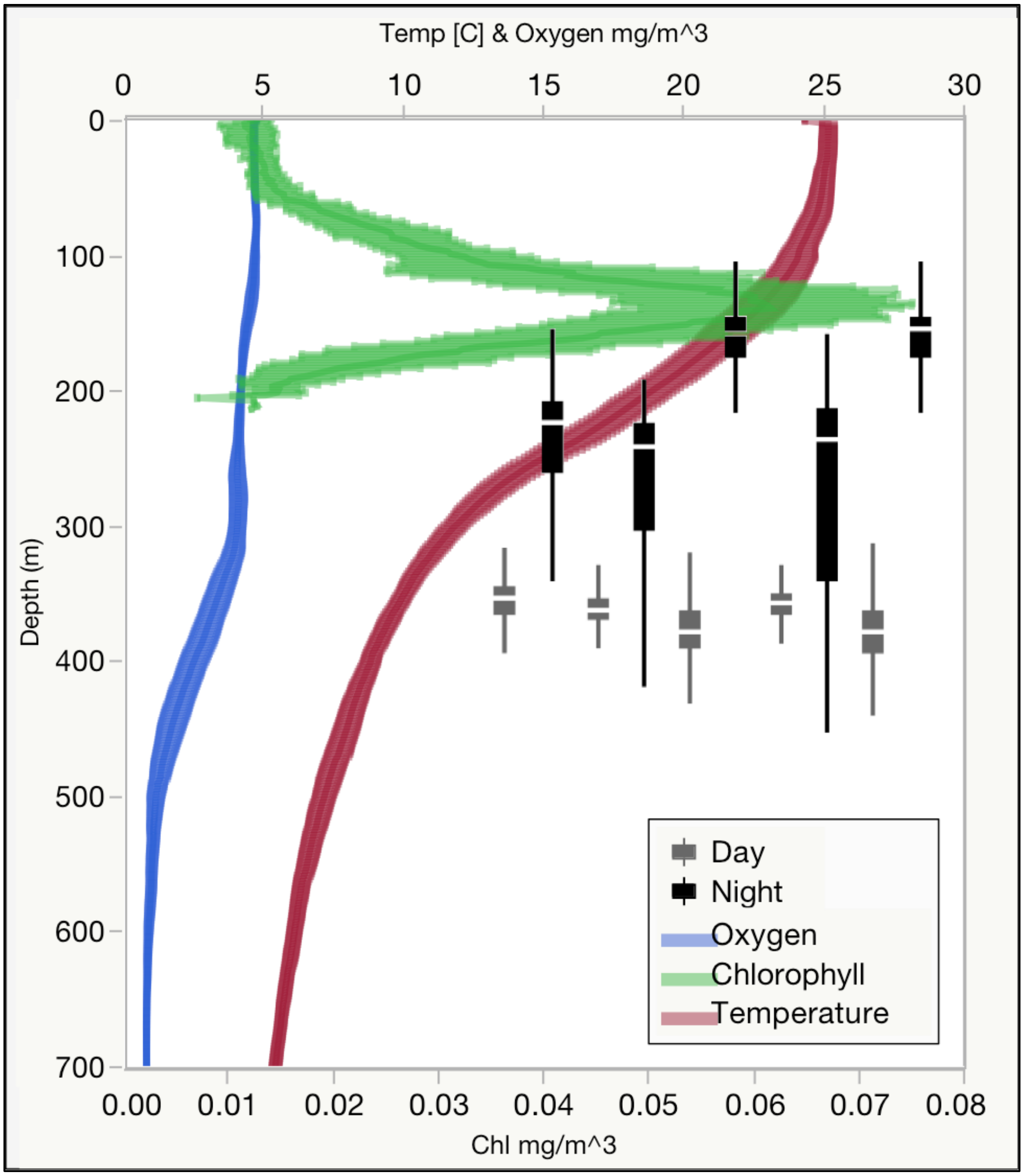

Figure S3: Depth, temperature, chlorophyll, and oxygen

Temperature, chlorophyll, and oxygen displayed as mean values ± standard deviation from 44 CTD casts on and around Cross Seamount in April 2008 (Data obtained from Reka Domokos and NOAA-PIFSC)

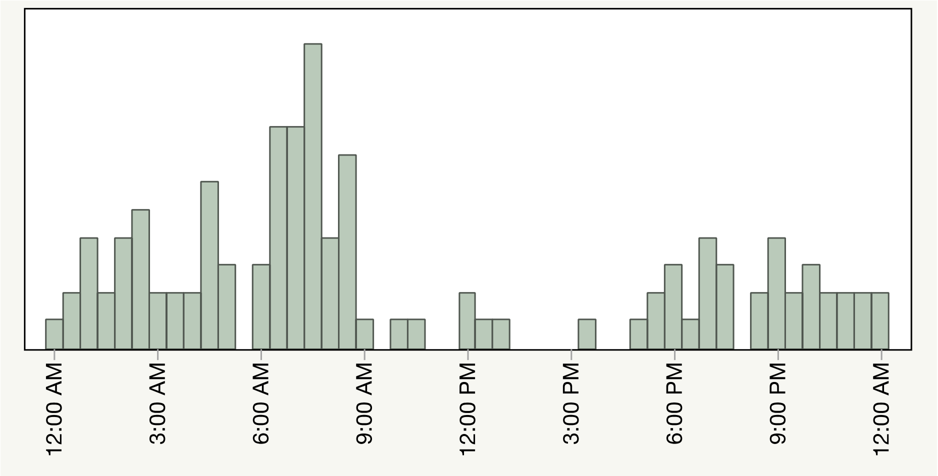

Figure S4: Swim time
Histogram of arrival times of rapid directed swimming events in. Swimming distances were 1.66-3.13km and all events occurred in less than 2 hours.

Supplementary tables

Table S1: Recapture summary
Due to the uncertainty of the actual capture date an estimate is given as the midpoint of the fishing trip in which the commercial vessel was fishing at Cross Seamount.

Tagging Date	Fish ID	Est. recapture date	Est. days at liberty	Archival tag?
4/9/10	184	2/25/11	323	No
10/2/12	403	10/15/14	744	No
10/4/12	237	7/15/13	285	Yes
10/4/12	413	1/15/14	468	Yes

Table S2: Depth
Depth values for all fish. ‘x’ indicates the depth sensor was bottomed out at 311m and accurate information was not available. Mean, SD, and maximum values for day and twilight as well as minimum values for day were not reported for v13 tagged fish.

	Day				Twilight				Night			
Fish ID	**Mean**	**SD**	**Max**	**Min**	**Mean**	**SD**	**Max**	**Min**	**Mean**	**SD**	**Max**	**Min**
164	-	-	-	-	-	-	-	144	252	38	x	121
173	-	-	-	-	-	-	-	233	258	28	x	212
175	-	-	-	-	-	-	-	190	261	27	x	188
177	-	-	-	-	-	-	-	223	263	30	x	198
178	-	-	-	-	-	-	-	123	172	28	291	97
179	-	-	-	-	-	-	-	216	263	33	x	191
180	-	-	-	-	-	-	-	235	261	25	x	194
182	-	-	-	-	-	-	-	225	270	23	x	211
184	-	-	-	-	-	-	-	115	170	28	x	103
185	-	-	-	-	-	-	-	276	286	39	x	165
191	-	-	-	-	-	-	-	271	299	20	x	206
192	-	-	-	-	-	-	-	232	279	24	x	206
194	-	-	-	-	-	-	-	233	265	24	x	201
195	-	-	-	-	-	-	-	230	274	29	x	196
237	-	-	-	-	-	-	-	126	189	36	x	94
239	-	-	-	-	-	-	-	235	286	27	x	199
248	-	-	-	-	-	-	-	233	277	33	x	191
249	-	-	-	-	-	-	-	253	255	31	x	209
252	-	-	-	-	-	-	-	171	299	30	x	63
400	361	22	462	310	321	61	425	178	240	49	405	157
401	365	18	454	306	338	53	421	227	259	53	438	194
403	377	23	479	264	259	74	425	120	165	34	429	95
410	365	23	458	310	341	54	429	178	261	66	454	161
413	380	29	487	260	255	72	429	107	157	22	413	103

Table S3: Swimming speed

Sustained swimming speeds for pairs of stations >2.5 km apart.

Stations	Receiver distance (km)	Detection radii distance (km)	Maximum Speed (km/hr)	Maximum Speed (FL/sec)
6 & 10	3.07	2.07	2.39	-
6 & 4	2.82	1.82	1.76	-
7 & 4	3.16	2.16	1.58	0.68
7 & 10	2.66	1.66	2.12	1.11
4 & 11	4.13	3.13	2.41	1.17
10 & 11	3.42	2.42	3.30	1.61

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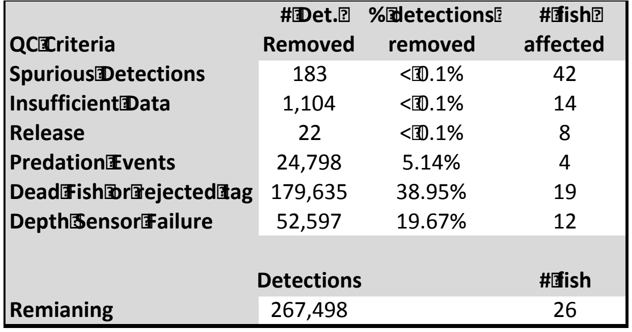
Appendices

Appendix-A: Quality control

Table: Quality Control
Quality control related removals of detections.



QC Criteria	# Det. Removed	% detections removed	# fish affected
Spurious Detections	183	< 0.1%	42
Insufficient Data	1,104	< 0.1%	14
Release	22	< 0.1%	8
Predation Events	24,798	5.14%	4
Dead Fish or rejected tag	179,635	38.95%	19
Depth Sensor Failure	52,597	19.67%	12
	Detections		# fish
Remianing	267,498		26

Removal Criteria Summary: Prior to analyzing vertical and horizontal movement data transmitters are filtered by this algorithm.

1. Spurious detections
    a. Single detections on the array in a 24-hour day→*Remove*
    b. Single detections above 100m depth in a 24 hour day→*Remove*
2. Insufficient Data
    a. Fewer than 200 detections→*Remove*
    b. Detections over duration less than 24 hours→*Remove*
3. Descent from tagging event
    a. First detection and consecutive detections of a descent, prior to sunset on the day of the tagging event, from 0-310.9m depth→*Remove*
4. Predation
    a. Sustained daily (24hr HST) epipelagic swimming followed by disappearance or stationary tag→Remove
5. Dead/Stationary tag
    a. Detected only on 1 receiver or on 2 receivers with overlapping detection ranges until end of tag life and no vertical movement →Remove
6. Depth sensor failure
    a. The sensor reads a constant depth (above 310.9m) for 10 consecutive detections→*Remove subsequent depth data*
    b. Vertical movement above 310.9m ceases completely→*Remove subsequent depth data*
    c. Failure of sensor to read below 310.9m for 48 hours→*Remove subsequent depth data*

1) Spurious detections

False detections can occur from code collisions, which arise when two tags transmit simultaneously within range of a VR2W receiver and incorrect data is recorded (Heupel 2006). In order to ensure the analysis of only real detections, transmitters that are recorded only a single time within the array over a 24-hour day (Hawaii-Aleutian Standard Time, HAST) are considered false detections and removed from analysis (Afonso 2012). Occasionally a spurious detection would consist of a depth record drastically shallower from all others between other detections in the day. For this condition single detections shallower than 100m and within a 24-hour period are considered false detections and removed from analysis. This process removed 183 detections from 41 different transmitter codes that matched *E. illustris* tags within the study site.

Removed:
Fish ID# (# detections removed, % total detections of the tag)

164 (3, 0.032%)
165 (2, 100%)
166 (2, 18.181%)
168 (1, 100%)
169 (2, 100%)
170 (3, 3.03%)
172 (1, 100%)
173 (12, 0.131%)
177 (2, 0.023%)
179 (2, 0.086%)
180 (1, 0.01%)
181 (2, 100%)
182 (2, 0.026%)
183 (2, 100%)
185 (1, 0.016%)
186 (1, 10%)
189 (1, 0.574%)
190 (3, 25%)
191 (25, 0.26%)
192 (1, 0.024%)
194 (1, 0.008%)
195 (1, 0.015%)
236 (1, 12.5%)
237 (4,)

238 (14, 0.274%)
239 (1, 0.001%)
240 (1, 100%)
246 (1, 100%)
247 (1, 100%)
248 (3, 0.105%)
249 (5, 0.165%)
251 (8)
252 (1, 0.032%)
253 (10, 0.177%)
254 (1, 100%)
255 (8, 0.125%)
401 (1, 0.051%)
403 (6,)
404 (42, 0.321%)
410 (7, 0.085%)
413 (1, 0.002%)
Total (183)
174, 175, 176, 178, 184, 188, 193, 197, 244, 400, 402 and 407 had no points removed.

2) Insufficient data

From a number of fish we received an insufficient amount of data for proper analysis. *E. illustris* with total detections under a 24-hour duration or fewer than 200 total detections were deemed to have an inadequate record and removed from further movement analysis. These criteria removed 14 fish from further analysis, 1,104 detections in total.

These criteria removed 14 fish from further analysis (numbers 166, 170, 174, 176, 186, 188, 189, 197, 236, 244, 402, 407 and 174.)

All detections removed due to < 200 detections:
Fish ID# (detections)
166 (9)
170 (96)
174 (304)
176 (55)
186 (9)
188 (143)
189 (173)
190 (9)

197 (72)
236 (7)
244 (4)
402 (54)
407 (169)
Total 13 fish (800) *corrected for 63 duplicates

Removed due to < 24 hours:
174 (304)

Grand Total 14 fish (1,104 detections removed) *corrected for 63 duplicates

3) Post-release descent behavior

Detections directly associated with the release of *E. illustris* from tagging procedures are not useful in analyzing *E. illustris* behavior and were removed from analysis. These detections of the descent were defined as any detection immediately following the release of a fish descending from the surface to 310m depth (extent of depth readings of the v13 tags). Up to 8 detections were removed for 8 individuals, in all cases contributing to 0.07% or less of total detections for the individual. In total 22 detections were removed accounting for less than 0.01% of total detections.

Removed:
Fish ID# (detections removed, % total detections)
164 (2, 0.02%)
175 (1, <0.01%)
179 (1, 0.04%)
184 (2, <0.01%)
191 (5, 0.05%)
192 (1, 0.02%)
194 (8, 0.07%)
195 (2, 0.03%)
Total (22, 0.005%)

4) Predation

With the combination of stress, physical strain, and release outside of their preferred benthic daytime habitat, recently tagged fish can be vulnerable to predation after release. If a tagged fish is eaten the tag will continue to send out acoustic signals as the predator swims around. If the predator shows markedly different behavior from the prey fish it can be identified and subsequent data removed. Predation events are identified by sudden and permanent changes in behavior and continued movement followed by disappearance of the tag or deposit of the tag on the seamount as the predator leaves the area or regurgitates the tag. Sustained epipelagic movements throughout the day are behaviors common in epipelagic predators that could prey on *E. illustris* such as epipelagic sharks. Capture and tagging can be traumatic for deep-water fish, which endure large pressure changes and an incision into the peritoneal cavity. Predation events are defined as sustained daily (24hr HAST) epipelagic swimming while maintaining horizontal and vertical movement and are followed by a disappearance or stationary tag. Subsequent detections were removed from analysis. Four fish succumbed to predation events and 56-100% of their detections were removed. Tags remained within the predators for 5-9 days (*M = 7)*. (Removes predation event from #179, 238, 253, 404).

Removed:
Fish ID# (detections removed, % total detections)
179 (1,297, 56%)
238 (4,942, 100%)
253 (5,636, 100%)
404 (12,923, 100%)
Total (24,798, 5.14%)

5) Dead fish/Stationary tag

To ensure the fish we are looking at are alive and the tag has not been rejected or the fish died, a fish that suddenly ceases to be detected on multiple receivers (or is detected only on receivers with overlapping detection ranges) and not displaying vertical movement is considered compromised and subsequent detections removed. All confirmed live fish (fish displaying vertical movement) displayed frequent horizontal and vertical movements and as insurance against tracking a dead fish those that ceased to move after tagging were removed. This removes errors from 19 fish. Using these criteria, some fish had a small number of detections 'trimmed' from the end of their last detections, and these situations were not necessarily indicative of death, but the rule was applied for consistency. (Removes errors from #164, 173, 175, 177, 180, 182, 185, 191, 192, 193, 194, 195, 237, 239, 248, 251, 252, 255 and 410). Using these criteria, some fish may have a small number of detections ‘trimmed’ from the end.

Removed:
Fish ID# (detections removed, % total detections)
164 (44, 0.48%) small trim
173 (26, 0.3%)
175 (92,081, 95.3%)
177 (2, 0.02%)
180 (11, 0.12%) small trim
182 (75, 0.1%)
185 (51, 0.82%)
191 (180, 1.88%)
192 (2, 0.05%) small trim
193 (7, 0.10%) small trim
194 (6, 0.05%) small trim
195 (16, 0.25%) small trim
237 (1, 0.01%) small trim
239 (84,082, 90.93%)
248 (6, 0.21%)
251 (21, 0.89%)
252 (41, 1.35%)
255 (2589, 40.52%)
410 (394, 4.86%)
Total (179,635, 38.95%)

6) Depth sensor failure

We experienced some failures of v13 depth sensors as they were pushed beyond their maximum rated depths and the tag manufacturer confirmed that the depth sensors in tags that exceed their depth rating are often damaged permanently. Failures observed included 1) flat-lining at a single depth, usually the maximum depth of 310.9m or -5m and 2) wandering through depths characterized by very gradual depth changes over a period of days. When false depth sensor readings were received the sensors were considered compromised and all subsequent vertical data for those fish was removed from the dataset. Based on what we know about *E. illustris* biology and what we have seen from fully functional v16 and archival tags (that did not descend below their maximum rated depths) we were able to identify false depth sensor readings from one or more of the following uncharacteristic fish behaviors. None of the following issues were experienced with v16 tags.

1) The sensor reads a constant single depth (above 310.9m) for 10 consecutive detections (2 fish).

2) Vertical movement above 310.9m ceases completely (2 fish).

3) Failure to of sensor to read below 310.8m for 48 hours (3 fish).

Pressure sensor data removed:
Fish ID# (detections with pressure sensor data removed, criteria #, % total detections)
164 (5,234, 3, 57.07%)
173 (7,794, 1 & 2, 85.87%)
177 (6,626, 1, 76.41%)
180 (4,327, 1, 46.62%)
185 (5,044, 2, 81.43%)
191 (3,460, 1, 36.90%)
193 (7,153, 2, 100%)
194 (4,870, 3, 41.75%)
248 (1,844, 1, 67.3%)
249 (2,094, 1, 75.95%)
252 (644, 1, 21.8%)
255 (3,527, 2, 100%)
Total (52,597, 19.67%)

Appendix-B: Extended introduction sections

Seamount ecosystems and the vulnerability of seamount communities

The classic definition of a seamount is an isolated topographic feature that rises over 1000m from the ocean floor without breaking the surface of the sea (Yesson 2011). Using this definition, over 33,000 seamounts have been identified and the worldwide estimate ranges from 39,000 to over 100,000 but it is clear that they are one of the largest, most widespread biomes in the world (Yesson 2011, Hiller 2007, Wessel 2010). A conservative areal estimate by Etnoyer (2010) based on 45,000 seamounts worldwide suggests that seamounts cover 28.8 million km^2, which is larger than South America or the world's continental shelves.

Within vast expanses of oligotrophic waters, seamounts can be areas of high productivity. Seamounts whose summits are shallow enough can be hotspots of predator biodiversity in the open ocean (Worm 2003) with tuna, bird, and marine mammal species found in at higher abundances over seamounts than away from the features (Morato 2008, Holland & Grubbs 2007, Campbell 2003). Diverse benthic communities frequently flourish on these isolates of suitable habitat (Richer de Forges et al. 2000). Benthic seamount communities have shown high rates of endemism of 10-50% and may differ considerably between clusters of seamounts along a single ridge system as well as by region (Stocks 2007, Richer de Forges et al. 2000). Trawl surveys show a heterogeneous distribution of seamount-associated ichthyofauna within and between ocean basins (Clark & Althaus et al. 2010).

Although fewer than 200 seamounts had been biologically surveyed by 2010 (Etnoyer 2010), many seamount fish and invertebrates have been heavily exploited, frequently in an unsustainable and destructive way (Koslow 2000, Niklitschek 2010, Foley 2011, Clark 2000, Clark & Koslow 2007, Clark 2009, Clark 2010, Roark 2009, Williams et al. 2010). Evidence shows that bottom-trawling on seamounts can cause severe damage to benthic fauna and a decrease in species richness and the abundance of bycatch, and may therefore change species composition on seamounts (Niklitschek 2010). Life history characteristics of many seamount fish and benthic seamount fauna make them highly vulnerable to fishing pressure and to damage from fishing gear (Morato & Clark 2007, Morato 2006, Koslow 1997, Roberts 2002). The combination of technological advancements, depletion of traditional fish stocks, increased demand for fish and discovery of deep water fish aggregations has caused the exploitation of fish populations that were previously out of reach or undesirable (Koslow 2000).

Many seamount-aggregating fishes have biological characteristics that make them intrinsically vulnerable to overfishing (Morato 2006). Historically, seamount associated and deep-sea fish species such as orange roughy (*Hoplostethus atlanticus*), pelagic armourhead (*Pseudopentaceros wheeleri*), Rockfish (*Sebastes* spp.), oreosomatids (*Pseudocyttus maculatu*s and *Allocyttus niger*), alfonsinos (*Beryx* spp.) and Patagonian toothfish (*Dissostichus eleginoides)* have been poorly managed and few trawl fisheries for these fish have been unsustainable (Koslow 2000, Clark 2010). Most targeted seamount associated species are a 'K' selected with high longevity, late maturity, low natural maturity, low fecundity and sporadic recruitment giving them a very low sustainable yield on the order of 1-2% per year (Morato 2006, Koslow 2001, Koslow 1996, Koslow 1997). Additionally, fish populations on isolated banks or seamount may have higher recruitment variability when compared to populations on adjacent shelf regions. Advection of larvae away from an isolated seamount results in the larvae accruing in pelagic waters with little chance of returning to settlement habitat. The same species inhabiting a shelf could have no local larvae retention and still be within a good location for settlement. For this reason, fish populations at isolated banks or seamounts may be more dependent on strong year classes for recruitment, more susceptible to overfishing, and have a slower recovery from overfishing than populations on adjacent slopes (Myers & Pepin 1994). Many seamount species form seasonal spawning aggregations making them an easy target for fishing, especially trawling (Clark 2000) and overexploitation is common wherever there is a commercial fishery (Clark 2000, Niklitschek 2010). The first seamount fishery for pelagic armourhead by soviet trawlers enjoyed landings as high as 200,000 tons in a year but ended in a commercial extinction of the species only 15 years after the fishery developed (Koslow 2001).

As near shore fisheries become less productive, fishermen are looking to deep-water stocks for new fishing opportunities. Allegedly sustainable fisheries for orange roughy, such as Chatham Rise in New Zealand may in fact be sustained by continued discovery of new fishing grounds and subsequent serial depletion (Koslow 2001). Depletions of Patagonian toothfish in the Southern Ocean have been obscured by fishery range expansions of the fishing fleet (Lord et al. 2006). Governments are sometimes willing to subsidize deep-sea fisheries to maintain fishery production and reduce pressure on local fish stocks. In Ireland, there was a rapid boom and bust in a subsidized orange roughy fishery, and in a span of only 5 years after opening, the fishery closed. Economic analysis suggests that without government aid the fishery would never have been economically viable (Foley 2011). Despite implementing a conservative quota and providing strict enforcement in Namibia, the aggregating orange roughy biomass declined markedly in all fished areas to only 10-50% of virgin biomass over a period of over only 6 years, although the reason for the decline is uncertain (McAllister 2002, Boyer 2001). Even with governments willing to try to manage seamount fisheries they can be particularly difficult to regulate with about half of all seamounts located outside of any exclusive economic zones (EEZs, Kitchingman 2007). Given the life history characteristics of deep sea fish, high costs of vessels, gear and fuel and the remote nature of seamounts and deep slopes, deep sea commercial fisheries for many popular food fish may not ever be economically and ecologically sustainable (Roberts 2002).

Residence time is an important metric for calculating maximum sustainable yield of a fishery and can be used to estimate the rate of removal of individuals from a population. Residence time is the amount of time a fish spends at a particular location prior to moving away, being captured, or predated on. This is important to consider for isolated populations (such as those on seamounts) with a fishery regularly removing individuals. Isolated populations can become depleted if the rate of removal of fish from a population exceeds the immigration and settlement rates.

Methods to study seamount-associated fishes

Studies of seamount-associated fish have mostly focused on illuminating general distribution patterns using sonar, submersibles or trawl sampling (Koslow 2007, Isaacs 1965, Misund 1997, Boehlert and Seki 1987, Parin & Prut'ko 1985*)* and until recently tracking fine scale behavior or individual residency has been unfeasible. Trawl surveys are excellent for collecting information on abundance, species composition, stomach contents, spawning condition and sex ratio but risk the destruction of benthic habitat such as deep-water coral beds which may have low resilience and extreme longevity on the order of millennia (Prut'ko 1985, Morato and Clark 2007, Norse & Watling 1999, Roark 2006, Roark 2009, Hall-Spencer 2002). ROV and submersible surveys can broadly sample benthic fauna and benthic fish species but they can be very expensive and infrequently observe more mobile fish—often the most commercially valuable species (Porteiro et al. 2013, Chave 1994). Sonar surveys are useful in assessing fish biomass in the water column, but species identification is challenging and the method has difficulties recognizing fish very close to the substrate (Godo 1994, Hjellvik 2003) or observing variability of migratory behavior seen in some species (Gaudreau 2000). In contrast acoustic tagging and tracking studies can provide detailed vertical and horizontal movement data and quantify residency with negligible environmental impacts. The method is relatively inexpensive and can be done aboard small vessels requiring only deployment and retrieval to collect year-long datasets illuminating the complexity and variability of fish behaviors (Weng et al. 2015).

Cross Seamount micronekton dynamics

E. illustris feed primarily on micronekton (Okamoto 1982, Prut'ko 1985, Parin & Prut'ko 1985) and while known to occasionally venture into pelagic waters, the strong preference for seamount and shelf habitat where micronekton often aggregate or accumulate indicates that particular micronekton dynamics may be important to *E. illustris* ecology. The phenomenon of enhanced micronekton abundance over seamounts has been repeatedly observed in Hawaiian waters (Boehlert and Seki 1984 , Sassa et al. 2002, Porteiro & Sutton 2007) with some micronekton species able to actively hold position over seamounts in strong currents (Wilson and Boehlert 2004) and even swim against strong currents upon descent (Domokos 2008). Holland & Grubbs (2007) hypothesized that there may be increased food availability for predators over seamounts and saw a significant increase in bigeye tuna stomach fullness when caught over Cross Seamount compared to pelagic caught bigeye tuna. Stomach contents over Cross Seamount consisted largely of seamount-associated micronekton with mean depth distributions of 200m or deeper.

There is some discrepancy whether Cross Seamount has increased micronekton abundance available to higher trophic levels at depths shallower than 200m. DeForest & Drazen (2009) observed a significantly lower abundance of micronekton over the plateau of Cross Seamount between 0-200m depth relative to pelagic waters and suggests it is due to active avoidance of the summit by micronekton as well as increased predation by pomfrets, alfonsinos and tunas (DeForest & Drazen 2009, Drazen et. al. 2011). Depletion of micronekton over seamounts by predators has also been suggested in other studies (Genin 1988, Genin & Dower 2007). However, bioacoustic surveys over Cross Seamount have observed higher abundances of micronekton throughout the water column. These micronekton displayed strong swimming abilities and were able to actively swim against currents as they descended during daily migrations (Domokos 2009). One explanation for the discrepancy between the two methods is that micronekton found over Cross Seamount are stronger swimmers than most pelagic micronekton and are able to actively avoid the 140m^2 Cobb trawl used in DeForest & Drazen's study leading them to conclude that there was lower abundance in the area. This trawl study found that micronekton above Cross at 0-200m consists primarily of juvenile epipelagic fishes followed by stomatopod larvae, mesopelagic fishes, crustaceans and cephalopods and there were at least two seamount associated species of micronekton (a myctophid *Benthosoma fibulatum* and cranchiid squid *Liocranchia reinhardti*) which were not found in pelagic waters away from the Cross summit. Examining only mesopelagic micronekton, about half are mesopelagic fish, 37% crustaceans and the rest cephalopods.

Cross Seamount has a micronekton regime distinctive from adjoining pelagic waters. While there have been reports of depleted open-ocean micronekton abundance over shallow and intermediate seamounts (Genin 2004, Boehlert 1988, DeForest & Drazen 2009, Drazen 2011), some seamounts have taxonomically distinct seamount associated micronekton species (Portiero & Sutton 2007) which may occur as a mesopelagic boundary layer community along the flanks of Cross Seamount during the day (Drazen et al. 2011). Bioacoustics surveys have identified a higher abundance of micronekton in the entire water column over Cross Seamount at night relative to pelagic waters only a few kilometers away with a conspicuous SSL in the top 200m and thick micronekton aggregations just over the seamount plateau (Johnston et al. 2008, Domokos). Cross seamount is a guyot, and both day and night micronekton aggregate over the plateau-like summit, which for the most part is at a depth of around 400m depth. This community, comprising higher biomass than pelagic waters, is likely sustained by the influx of planktonic organisms that are unable to swim against strong currents impinging on the seamount. Additionally, a relatively thick deep scattering layer (DSL) on the flanks of Cross Seamount extending 2-5 km away from the seamount has been identified and likely consists in part of a taxonomically distinct mesopelagic boundary community (Domokos 2008). Typically in pelagic waters of the Geologists seamounts region, deep and shallow scattering layers consist of diverse assemblages between 20-200m and 500-800m depth respectively (Domokos 2009).

Secondary production

Upwelling nutrients and water entrapment by taylor columns over seamounts has been suggested as a driver for increased productivity and fish biomass at seamount habitats (Taylor 1923, Huppert & Bryan 1976). However, increased local primary production is unlikely able to support higher fish biomass on seamounts due to the transient nature of upwelling events (Genin & Dower 2007, White et al. 2007, Morato 2009) and often times there is not even measurable chlorophyll (Gennin & Bohlert 1985, Genin 1987). However, zooplankton may be drawn by currents over seamounts from surrounding pelagic waters (Domokos pers. comm) and provide a more concentrated food source for local micronekton than surrounding pelagic waters. This is essentially 'bottom up control' of the foodweb with increased production based on increased secondary rather than primary production.

Appendix-C: Supplementary analysis, results and discussion

Directional Movement

Methods

Models and CTD observations at Cross Seamount indicate a predominantly anticyclonic (clockwise) current around the plateau (Domokos 2009), and we might expect it to influence the movements of *E. illustris* at the seamount in the same direction. Movement between acoustic receivers was assessed for directional preference. Movement events between pairs of stations on the periphery of the seamount (Cohort 1: 1-7, 4-10, 6-7, 7-10; Cohort 2: 1-7, 4-10, 4-5, 5-6, 6-7, 7-10; Cohort 3: 10-11, 4-10) was designated as 'clockwise' or 'counterclockwise' and a Wilcoxon test used to determine if there was a predominant directionality. Movement events were defined as consecutive detections of a fish at these station pairs and the number of movement events for each fish at each station pair were used for the analysis. Stations not used for this analysis (2, 3, 8, 9) were removed prior to identifying movement events. Simultaneous detections were removed prior to analysis.

Results

There was no significant directionality of movement detected between the stations along the periphery of the seamount. Overall there were more clockwise movements for 5 of the 7 station pairs examined as well as all stations combined (1085:803), but no significant differences

($p > 0.05$).

Reports of currents around Cross Seamount are varied with observations of highly variable currents which fluctuate on time scales as short as half an hour (Domokos 2007) and reports from fishermen of periods of high currents lasting weeks. While the tagging data hints at a preference in clockwise movement around the seamount the prevalence of both clockwise and counterclockwise movements indicate that the mean current is not strong or sustained in a cyclonic or anticyclonic flow and/or the fish movements are independent of the currents. Since the micronekton prey of *E. illustris* may have their movements encouraged by the prevailing current, it might be preferential for *E. illustris* to swim against the current at times to increase prey interactions. Additionally if there is advection of pelagic micronekton over the seamount, swimming into the current would position the fish in a preferential foraging position closer to the source of the micronekton.

Recaptured fish

Results

A commercial fisherman aboard F/V *Hoku* recaptured fish 184 at Cross Seamount in late February 2011 after a total time at liberty of approximately 323 days. Acoustic data for this individual encompassed the entire duration of the battery life, 177 days. The tags were returned without the fish so sex and fork length at recapture were not reported.

A commercial fisherman aboard F/V *Ao Shibi IV* recaptured fish 237 at Cross Seamount in mid July 2013 after approximately 285 days at liberty. This fish was tagged with a v13 and an archival tag on October 4, 2012 and acoustic data encompassed October 9, 2012 to April 7 2013, a duration of 185 days and the entire extent of the v13 tag battery life. The tags were returned with only a partial carcass so weight and fork length at recapture were not reported.

A commercial fisherman aboard F/V *Kaimikai* recaptured fish 413 at Cross Seamount mid January 2014 after approximately 468 days at liberty. Acoustic data for this individual began December 30, 2012 ninety days after the individual was tagged and continued until the acoustic receivers were removed October 10, 2013. The entire fish was returned and the incision where the tag was inserted was completely healed with no scarring on the outside of the body. The individual was determined to be a male with a fork length of 71 cm.

A commercial fisherman aboard F/V *Vicious Cycle* recaptured fish 403 in mid-October 2014. This male was tagged with a v16 and no archival tag and recaptured at 62 cm FL, an increase of 5 cm from the original capture date approximately 744 days earlier on October 2, 2012. Acoustic data for this individual encompassed the entire 371 day duration that the tag and acoustic receivers were deployed together (10/06/2012 to 10/11/2013).

Best attempts were made at informing and enticing Cross Seamount fishermen to return whole tagged fish, but it is always possible that some fish were recaptured and not turned in. Two recaptured fish were not immediately identified and one made it to the auction floor before being noticed and the other sold to a processor and was cleaned before anyone noticed it could be returned for a cash reward.

Hourly detection rate

Results

If detection rates were equal throughout the day we would expect 4.17% of a day's detections to occur each hour. Proportion of total detections by hour of the day, tends to be lower than expected between 0600-1900 and higher 1900-0600 (**Figure A1**).

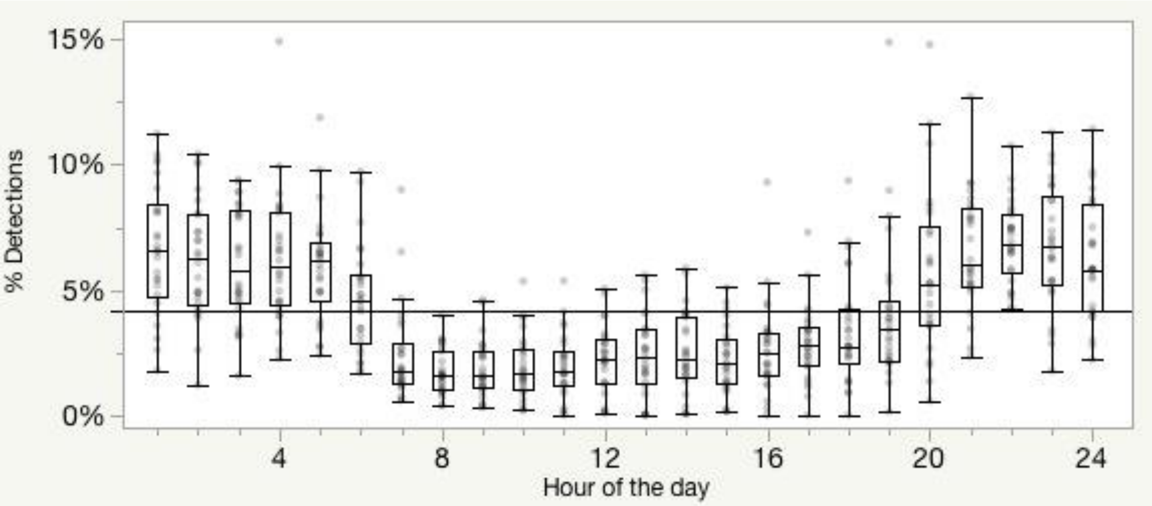


Figure A1: Percent detection by hour
Boxplot of the percent of detections per hour for each fish. Each point indicated percent detections per hour for one fish. Horizontal line indicates the expected value if detections were spread evenly throughout the day

Temperature at Cross Seamount Plateau

Method

Temperature was recorded using an archival tag (Lotek Wireless, Ontario, Canada) May to October 2012 on the plateau of Cross Seamount at a depth of 406 meters at acoustic receiver station 10 on the North side of the plateau of Cross Seamount.

Results

Water temperature at a depth of 406 m at station 10 was recorded from mid May to early October 2012. Overall, temperatures had a normal distribution with a mean of 8.3 +/- 0.6 SD °C and ranged from a maximum of 9.8 °C to a minimum of 6.7 °C. Average temperatures dropped sharply from 8.7 +/- 0.4 °C in May-July to 7.8 +/- 0.4 °C in August through the beginning of October. Throughout the day the mean temperature reached its lowest value (8.19 +/- 0.04 °C) at 3:30am and highest value (8.43 +/- 0.5 °C) at 5pm. The daily temperature range was 0.62 to 1.88 °C (with a single anomalous day at 2.5°C) and the mean daily temperature range was 1.20 °C +/- 0.34°C (**Figure A2**).

The temperature on the plateau of Cross Seamount was relatively stable around 8.3 °C over the 5 month duration of the tag deployment with a standard deviation of only 0.6 °C from the mean and a total range in temperature of 3.12 °C. The drop in mean temperature between July and August was only 0.9 °C, which was less than the average daily fluctuation in temperature. Daily temperature fluctuations were relatively small (usually < 2°C) especially when compared to the temperature range the fish undergo during DVM. No clear patterns in temperature were identified that would likely affect the behavior of the fish.

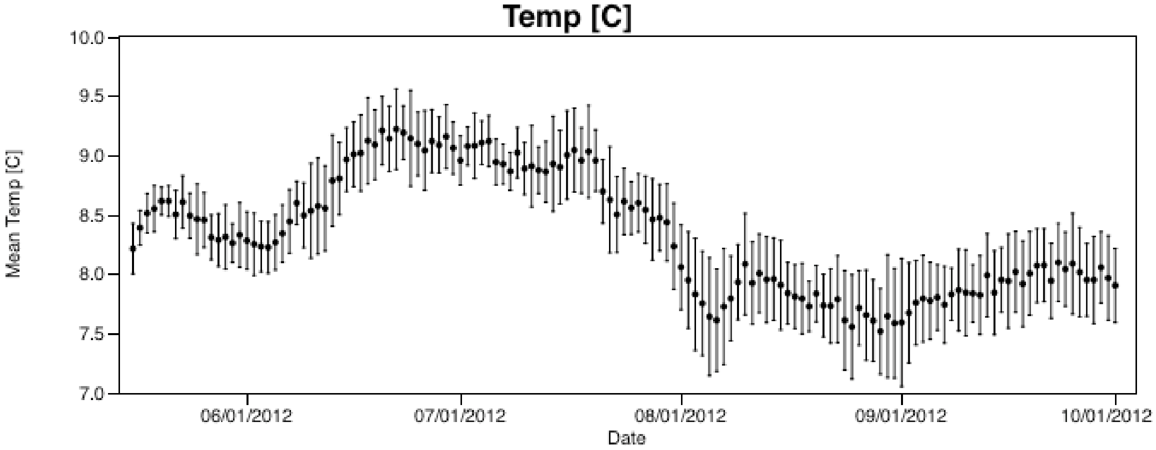


Figure A2: Temperature
Daily mean temperature on the plateau of Cross Seamount. Error bars are 1 standard deviation from the mean.

Vertical distribution response to lunar illumination

Method

Light intensity is a common stimulus controlling vertical distributions of mesopelagic fauna (Salvanes & Kristoffersen 2001) and based on current understanding of the ecology of mesopelagic and seamount fishes, we might expect to see diel vertical migratory behavior with mean nighttime depths positively correlated with lunar illumination (the fish stay deeper when there is more light). In order to calculate the correlation between lunar illumination and depth, the mean and minimum nightly depth was plotted against lunar illumination and a linear least squares regression was calculated for fish showing vertical data of at least 15 days (over half of a lunar cycle, n=17). A regression effect was deemed significant if $p < 0.05$. Mean and minimum depth values for this were calculated by averaging all detections of each fish from 2300-0100 hours each night they were present. Lunar illumination values were the proportion of lunar illumination at midnight and ranged from 0 to 1. For regression analysis individual fish were weighted by number of depth values so that each fish had equal influence on the regression regardless of number of days present at the seamount.

Results

Out of 17 fish with vertical data over half of a lunar cycle, individual fish showed a variety of significant correlations ($p < 0.05$) between lunar illumination and mean depth. Seven fish, including all fish with shallower depth preferences, had negative correlations, two fish had positive correlations, and eight fish had no significant correlation (**Table A1**). Together, the fish with shallow nighttime preference (184, 237, 403, 413) had a strong significant correlation ($p < 0.0001$) between lunar illumination and depth. Fish 178, which also had a shallow depth preference, was left out of the analysis because it was not present for over half a lunar cycle. Overall the fish with deep nighttime preference had no significant correlation**.** Similar results were seen using minimum nightly depth vs lunar illumination except that fish 164 and 195 showed no significant correlation between depth and lunar illumination. Lunar illumination explained 10% of the variation of mean depth and 13% of the variation of the minimum depth.

Table A1: Lunar illumination
Results of regression analysis between lunar illumination and mean depth. Bold indicates significant values.

Fish	Slope	DF	F-ratio	R^2	P-value
164	+	**1,17**	**5.084**	**0.23**	**0.038**
175		1,16	0.022	0.00	0.884
180		1,20	2.953	0.13	0.101
182		1,31	2.480	0.07	0.125
184	**-**	**1,130**	**13.183**	**0.09**	**< 0.001**
191	**-**	**1,20**	**7.076**	**0.26**	**0.015**
192		1,16	1.091	0.06	0.312
194		1,23	0.592	0.03	0.449
195	+	**1,28**	**6.583**	**0.19**	**0.016**
237	**-**	**1,72**	**6.378**	**0.08**	**0.014**
239	**-**	**1,32**	**7.723**	**0.19**	**0.009**
252		1,7	0.271	0.04	0.619
400		1,20	0.928	0.04	0.347
401		1,7	1.129	0.14	0.323
403	**-**	**1,208**	**26.030**	**0.11**	**< 0.0001**
410	**-**	**1,31**	**6.261**	**0.17**	**0.018**
413	**-**	**1,182**	**32.012**	**0.15**	**< 0.0001**
Shallow	**-**	**1,598**	**67.436**	**0.10**	**< 0.0001**
Deep		1,292	0.152	0.00	0.697

Mesopelagic fishes may follow certain light intensities in order to avoid predation and remain within prime foraging conditions (Gautier & Rose 2002, Kaartvedt et al. 1996). We expected *E. illustris* to have a positive correlation between mean or minimum depth and lunar illumination. *E. illustris* have extremely large eyes and are almost certainly a visual predator. However, the average nightly depth of most fish was independent of lunar illumination indicating that many individuals do not follow an isolume. Perhaps the relative changes of light intensities or other daily cues, prompt DVM behavior in *E. illustris* and a collection of other environmental conditions that modify fine scale behavior like nightly depth preference such as oxygen concentration, temperature or food availability (Ringelberg 1995). Bioacoustics surveys suggested that micronekton layer positions in the water column over Cross do not appear to change with lunar illumination (Domokos pers. comm.) and *E. illustris* may be choosing depth preference based on prey availability or preference. In contrast, all five individuals with shallower nighttime depth preference did show a correlation between lunar illumination and mean or minimum depth with 10-13% of vertical variation explained by the lunar illumination. Light from the moon can help some fish detect prey and by seeking out particular light intensities the fish can forage more effectively or find more preferred prey.

There was considerable variability between individual fish when it came to correlation between lunar illumination and mean depth. As a group the fish with the deeper depth preference showed no correlation between lunar illumination and depth, but three individuals had a negative correlation, just as the shallower fish did, suggesting that even with nighttime depths around 270m the light from the moon can influence behavior, and affect visual feeding.

Unexpectedly, two fish (182 & 164) showed a significant positive correlation between mean depth and lunar illumination explaining 7-23% of the variation in mean depth. 'Reversed' diel vertical migration, different from this example in that the organisms swimming deeper at night rather than shallower during increased lunar illumination has been shown to decrease predation in copepods (Ohman et al. 1983), but reasons for these much larger fish to seek out different light intensities each night are unclear. With such variation in vertical behavior observed it is not unreasonable to think that this pattern may be real, however when using minimum depth these two fish showed no significant positive correlation while all other fish showed the same pattern.

Internal Temperature

Method

Archival tags implanted in a subset of the fish were able to record the internal temperature of the fish every 5 minutes. This information can help determine whether temperature is a driving force in the vertical movements of *E. illustris* rather than food availability. Temperatures were compared between fish as well as between daytime and nighttime depths.

Results

Internal temperatures were generally 6.2-9.6 °C during the day while the fish were in deep water and 16.6-22.8 at night when they were in shallow water. For both fish 413 and 237 the minimum internal temperature was 5.8 °C and the maximum was 24.5-25.9 °C (**Figures A3 & A4, Table A2**). Average daily temperatures were 6.9 °C and 8.2 °C for fish 413 and 237 respectively during the day and 19.9 °C and 20.6 °C during the night. Temperature was strongly correlated with depth for 237, 413P and 413S with depth accounting for 96% of the variability (**Table A3**).

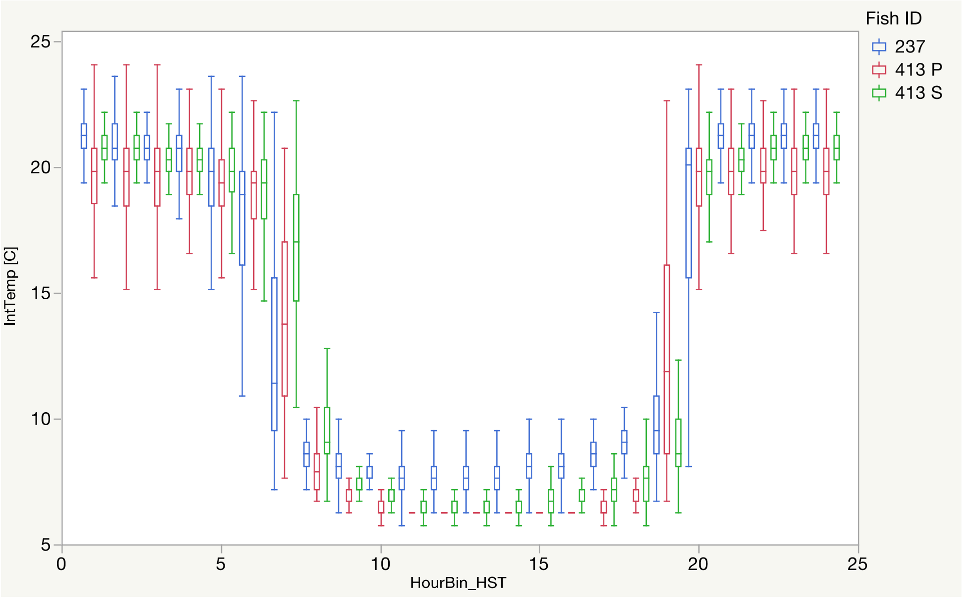


Figure A3: Internal temperature
Internal temperature of fish 237 and 413P (pelagic state) and 413S (seamount associated) by hour of the day

Table A3: Internal temperature
Internal temperature measurements for fish 237 and fish 413 at Cross Seamount (413S) and when it was absent from the seamount, likely in the pelagic environment (413P) for absolute minimum and maximum as well as average and standard deviation of daytime temperature and nighttime temperature (nautical twilight excluded).

Internal temperature [°C]						
Fish ID	**Min**	**Day**	**SD**	**Night**	**SD**	**Max**
237	5.8	8.2	0.4	20.6	0.7	24.5
413 P	5.8	6.7	0.4	19.7	1.2	25.9
413 S	5.8	7.2	0.3	20.2	0.7	23.6

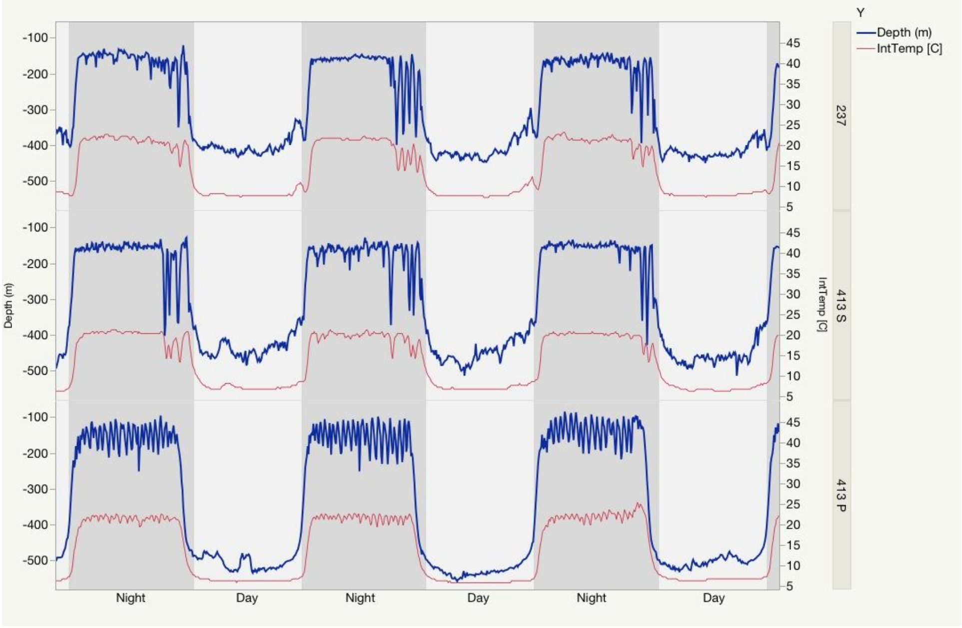


Figure A4: Archival depth and temperature profile
Three nights and three days of depth and internal temperature of fish 237, 413P (pelagic state) and 413S (seamount associated).

Table A4: Temperature vs Depth
Results of least squares regression analysis of mean depth and temperature.

Fish	DF	F-ratio	R2	P-value
237	1, 6681	159,138	0.96	<0.0001
413P	1, 2049	49,981	0.96	<0.0002
413S	1, 1554	35,643	0.96	<0.0003

Most fish are ectothermic, but endothermy has been observed in a variety of species of fast moving fish such as tunas, lamnid sharks and billfish as well as the moonfish. The elevated temperature is often confined to certain regions of the body that provide the greatest benefit to the fish such as red muscle, brain and eyes. This regional thermoregulation can increase fitness of fish in low or variable water temperatures by increasing reaction times and improving foraging capabilities (Graham 2001, Carey 1982). Swordfish, which don't undergo continuous movement like tunas are able to retain heat in the eyes and brain to increase and stabilize the function of the central nervous system (Carey 1982). Retaining heat at levels greater than the ambient water temperature can be valuable for mesopelagic fishes and regional endothermy as well as full-body endothermy has been observed in vertically migrating mesopelagic fishes. Recently, whole body thermoregulation of a mesopelagic fish was discovered. Using heat derived from constant pectoral fin movement and a series of efficient heat exchanging mechanisms the opah (*Lampris guttatus)* is able to retain heat greater than the ambient temperature of the water in the majority of the body (Wegner 2015). If *E. illustris* were able to retain body temperature greater than the ambient water temperature it could receive a great advantage in foraging by elevating reaction time and CNS function. From the current study it is clear that the whole body temperature of *E. illustris* is highly variable and drops to the temperatures of the water over the plateau, or lower when swimming deeper. While it is possible that the fish retain elevated temperatures in certain vital regions of the body it is beyond the scope of this study to determine that and would require in situ measurements of certain tissues within the fish as well as investigation of the countercurrent heat exchange mechanisms necessary for fish to keep from losing too much heat from the gills. However, based on the temperature of the peritoneal cavity we can conjecture the relationship between temperature and function of *E. illustris*.

The internal temperature of the fish is highly variable and strongly dependent on the depth of the fish. When the fish spends time at deeper depths during the day the internal temperature can drop to below 6 °C and remains low until the fish ascends at night and enters warmer water where it can reach temperatures above 22 °C. The internal temperature the fish is strongly correlated with depth and the fish are able to function adequately at each end of this extreme temperature range. There is no indication of attempts at behavioral thermoregulation with daytime temperatures remaining continuously low around 7°C and only moderate variations in temperature of a few degrees at night. Clearly the temperature within the fish is responding to the water temperature and the diel vertical migrations that the fish undergo nightly take the fish from below the thermocline to above it on a daily basis. The large range of temperatures experienced throughout diel vertical migrations indicates that temperature is probably not constraining the vertical movement of the fish.

However, daily vertical migrations may be driven in part by enhanced energetic efficiency. Improving bioenergetics by feeding in warm water and moving to colder water to rest and digest is one of the most often referenced driving forces for DVM behavior and is the driving force for male dogfish (*Scyliorhinus canicula*) vertical migrations in Ireland, reducing energy costs by ~4% (Sims et al. 2006). While the DVM behavior appears to be driven by food availability with increased feeding opportunities by following micronekton movements, the energetic benefits of feeding in warm water and resting in cool water could be a substantial advantage to making nightly vertical migrations across the thermocline. Elevated temperatures experienced by the fish during the night may improve the function of the central nervous system and allow the fish to forage more effectively and increase the capacity for movement as indicated by the observed greater horizontal movements at night in warm water than during the day in much colder water. It is clear that undergoing vertical migrations each night is an important part of *E. illustris* ecology. The possibly obligate ascent to warmer waters at night may be important because the fish experience a combination of increased forage as well and increased ability to catch prey in the warmer waters, and then are able to digest and rest in deeper waters where the temperature supports reduced energy costs.

Archival Depth

Method

Understanding how *E. illustris* benefit from the seamount topography can be elucidated by observing them away from the seamount, possible for double-tagged fish with both acoustic and archival tags. In order to understand how *E. illustris* feeding behavior changes when away from the seamount daytime and nighttime depths were compared between the two environments. Based on acoustic data it is possible to determine if a fish was present or absent from the seamount. For a fish that was absent from the seamount comparisons in archival depth data were made between time at the seamount and time away. A Welch's unequal variance t-test was used to determine if there was a difference in depth between seamount associated and non-seamount associated pelagic states. A consistent depth record every 5-minutes allowed fine scale nighttime movements to be observed and we used a Welch's test for unequal variance to determine if the variance in depth changes by hour bin through the night. This was followed by a Tukey-Kramer HSD post hoc test to determine when the fish showed the greatest variation in depth.

Results

Two fish that were recaptured with archival tags recorded depth and internal temperature at 5-minute intervals. Prior to analyzing any data all records from tagging to 48-hours after release were removed (413: 875 records; 237: 750 records) as well as after 12 hours prior to recapture and afterwards (237: 8,025 records) to remove any potential unnatural behaviors caused by tagging or capture. Fish 237 had 80,175 records for 278.4 days of data and fish 413 had 43,268 records covering 150.2 days.

After release a large gap in acoustic data indicated that fish 413 left the vicinity of the receivers immediately after being tagged returned 88 days later, at which point the fish returned and was recorded on acoustic receivers. While it's unknown where the fish was during this time, it is clear that it was in the pelagic water for some time. For this reason, some analyses of that fish are split between the two habitats and reported as 413P for pelagic and 413S for seamount.

Fish 413P (pelagic) is tracked for 88.9 days from 48 hours after release (25,599 records) and 413S (seamount associated) is tracked for 64.8 days (18,669 records) beginning on December 30, at 18:19 when the first acoustic transmissions were received until the archival tag battery died.

Fish 237 and 413S tended to have increasing variation in depth as the night progressed (Fish 237: F(23, 29021) = 62,640, p<0.0001, Fish 413S: F(23, 6752) = 19,950, p<0.0001). Fish 237 had significantly greater mean hourly variance in depth between 0300-0700 than any other time in the night while fish 413S had significantly greater mean hourly variance in depth between 0400-0700 than any time in the night before 0300. In contrast, when fish 413 was pelagic it did not show obvious increased vertical deviations and the only significant difference in variance was a peak at 0400-0500. After the long ascent to shallower waters the two fish generally begin the night with very small vertical deviations in depth, possibly feeding on a thin layer of micronekton. A few hours before sunrise the two fish tended to make a series of deeper dives, sometimes reaching depths beyond 400m before making a final descent to daytime depths.

When away from the seamount fish #413 had deeper average nighttime ($p = 0.045$) and daytime ($p < 0.0001$) depths than at the seamount (**Table A5).** Both fish had consistent nightly vertical migrations regardless of association with the seamount.

Table A5: Archival depth
Mean and standard deviation for depths during day, twilight and night as well as absolute maximum and minimum depths for fish 237 and fish 413 at the seamount (S) and away from the seamount (P). Depth summaries are calculated only from archival tags.

	Day		Twilight		Night			
Fish ID	**Mean**	**SD**	**Mean**	**SD**	**Mean**	**SD**	**Max**	**Min**
237	401	33	264	81	168	37	573	64
413 P	497	31	286	78	182	40	591	70
413 S	457	40	273	80	174	38	607	109

For both fish 237 and 413S the nighttime profile was generally very flat at the beginning of the night and then became punctuated with large vertical movement before descending. The final descent was relatively rapid, but repeated changes in vertical direction starting around 350m indicated that the fish may be following the contour of the seamount down, or perhaps feeding as they descend. In contrast fish 413P usually has a direct descent to beyond 500m with few deviations in vertical direction. During the day 413S and 237 have a more or less sawtooth profile while 413P has a much smoother profile and may be indicative of a lack of bathymetric features. After returning to the seamount, fish 413 left the seamount for ~29 hours while simultaneously tracked with acoustic and archival tags. The fish departed the acoustic array in the early evening and showed normal behavior through the night until right before sunrise where it made two unusually deep descents before the final descent. The following daytime behavior was similar to earlier pelagic behavior with greater depth and a U-shape profile. The most notable deviation from normal behavior occurred the following night when the fish had very large depth amplitude, swimming between about 200m and 400-450m repeatedly until returning to the seamount (as indicated by acoustic detections) at which time the erratic swimming immediately stopped and normal seamount behavior resumed. It is possible that these deep dives were an attempt to locate the seamount. Fish 237 also left the seamount on a number of occasions for 2-3 days at a time but showed no obvious difference in behavior from when it was on the seamount. This could indicate that there is very different individual behavior, as we have already seen in site and depth preferences, or it's possible that the fish was still at the seamount on the western plateau and was never detected on the acoustic array during those time.

Vertical migrations occurred every single night regardless of whether the fish was at the seamount or away. It is clear that vertical migration to shallower depths at night are extremely important for the fish. Even directly after tagging both fish 237 and 413 showed a weak attempt at vertical migration. The two fish had almost identical behavior spending the first day around

300-350m depth, much shallower than their typical daytime depths, but made an attempt at vertical migration with an ascent to around 200m and then back to 300-350m for the second day, resuming normal behavior on the second night. It is clear that these fish were affected by the tagging process and unable or unwilling to undergo normal DVM behavior as was seen in subsequent days, and it is notable that the altered behavior resulted in a shift in depth to shallower waters.

The vertical behavior of fish 237 and 413 at the seamount was extremely similar, very repetitive and predictable and adds a lot of insight into the daily vertical movement patterns of the species. However, it is important to note that acoustic data showed quite a bit of variability between individual fish in depth preference (both day and night) and daytime residence and both of the archival-tagged fish are in the minority for these behaviors.

The archival data confirms that the acoustic data at the seamount gave an accurate portrayal of vertical movements undergone by fish 237 and 413. Acoustic depth data from fish 237 was constrained by the depth range of the v13 tag and this resulted in loss of useful daytime depth data and an abridged twilight depth profile. However, even with these constraints the average twilight depths between the two tags were not too different with 260 +/- 60 SD and 264 +/- 81 for acoustic and archival respectively. Fish 237 had slightly differing nighttime depths between the two tag types (189 +/- 36 and 168 +/- 37) but no major discrepencies. At the seamount fish 413 had similar twilight and nighttime depths (twilight: 255 +/- 72 & 272 +/- 80, night: 157 +/- 22 & 173 +/- 38) for acoustic and archival tags respectively. The archival tag was able to record deeper daytime depths than the acoustic tag when the fish was over the slope of the seamount out of acoustic coverage and consequently the average daytime depth was deeper as recorded by the archival tag (acoustic = 380 +/- 29 archival = 457 +/- 40). This loss of the deepest extent of the fish's range may not be an issue for other v16 tagged fish (fish 400, 401, 410) that tended to spend days over the plateau of the seamount rather than over the edge in deeper water.

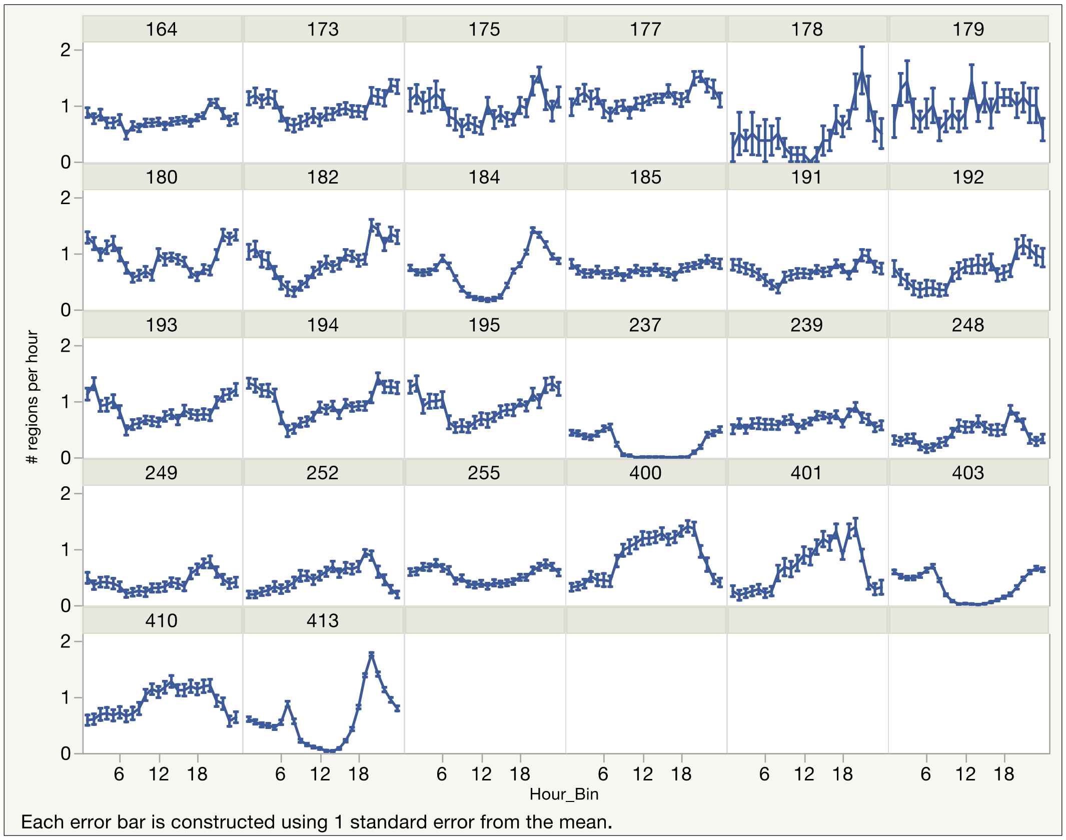
Hourly activity

Methods

'Hourly activity' was calculated as the mean number of regions visited per hour for each day present on the seamount and was plotted for each fish to observe their activity level throughout a 24-hour day.

Results

To visualize individual activity level throughout a 24-hour day hourly activity was plotted for each fish (**Figure A5**). The hourly activity between 1000-1600 was lowest for the 5 fish with shallow nighttime behavior (178, 184, 237, 403, 413). Between 1900-2100 half of all fish had their highest rates of activity and between 1800-midnight over 77% of all fish had their highest hourly activity rates. The reason for the activity peak is unclear and appears to vary by individual.



Each error bar is constructed using 1 standard error from the mean.

Figure A5: Hourly activity
Average number of regions per hour for each hour for each fish. Average values are calculated for all days the fish were present on the seamount. Error bars are one standard error from the mean.

Seamount habitat utilization

Results

Daytime occupancy: Twenty-one fish showed occupancy at the middle region more than any of the other regions for 49-97% of days tracked. In the middle region 14 fish showed residence for over 80% of days detected, nine of which showed residence for over 90% of days detected. Two fish showed clear occupancy at the North region (178, 63%; 413 93%) and one in the SW region (403, 58%). Twenty fish showed zero occupancy at 1-2 regions but all 26 fish showed some occupancy at the middle region (minimum, fish 184, 2%). A few fish had the majority of daytime occupancy at 2 or more regions (fish 175, 184, 192, 237, 255), possibly having a number of preferred areas in different areas of the seamount. Averaged over all fish 69% of occupancy was in the middle region, followed by North and Southwest (13%, 12% respectively) and East (6%). Average occupancy time per day for each fish was 0.37 to 9.62 hours (*M* = 5.96, *SE* = 0.61).

Occupancy values and average time at a region are greater during the day than night but there is individual variability in the strength of occupancy as well as location preference. Fish 184 utilizes daytime habitat primarily in the Southwest (41.1%) or North (50.9%) for extended periods of time up to 28 days before switching to the other region, despite the ability to move between the 2 areas (a distance of 2.07km) in less than an hour.

Nighttime occupancy: Twenty-one fish showed nighttime occupancy at the middle region—more than any of the other regions—for 43-95% of nights tracked. In the middle region three fish showed residence for over 80% of days detected, with only one that showed residence for over 90% of days detected. All fish had at least a quarter of their occupancy at the middle region except for one, which had clear occupancy at the East region (173, 47%). Ten fish had zero occupancy at 1-2 stations but all had occupancy in the middle region (minimum, fish 173, 24%) and only one fish (179) had zero residence in the East region. Averaged over all fish, 56.5% of occupancy was in the middle region, followed by East (25.5%), Southwest (12%) and North (6%). Average occupancy time per night for each fish was 2.50 to 8.57 hours (*M* = 4.74, *SE* = 0.52).

The East region appears to be unimportant daytime habitat but important nighttime habitat. During the day the average occupancy in the region was only 6% with nine fish showing zero occupancy in the area and only two fish showing over 25%. In contrast, at night only one fish, with only 7 days of data, had zero occupancy (179), and 12 fish had over 25% of their occupancy in the region with an average for all fish of 26% occupancy at night. The North region appears to be less important nighttime habitat with a maximum occupancy for any fish of only 18% and the middle region continues to be the most important habitat at night for most fish, with an average occupancy of 57%.

During each of the days detected, fish visited 1-4 regions with daily activity of 1.16-2.52 (*M* = 1.94) regions during the day and 1.5-3.16 (*M* = 2.48) regions at night. Horizontal activity slowed during the day but remained well above 1 on average indicating that the fish are still moving significant distances even when they are not up in the water column. All but two fish (185 & 248) had greater activity during night than during the day. To visualize individual activity level throughout a 24-hour day hourly activity was plotted for each fish. The hourly activity between 1000-1600 was lowest for the 5 fish with shallow nighttime behavior (178, 184, 237, 403, 413). Many of the fish had a peak in activity in the early evening Between 1900-2100 half of all fish had their highest rates of activity and between 1800-midnight over 77% of all fish had their highest hourly activity rates. The reason for the activity peak is unclear and appears to vary by individual.

Time of departures from seamount

Method

Just as detections on receivers within an acoustic array provide information on the behavior of a fish so do gaps in detection with the length and frequency of the gaps indicative of leaving the seamount or array. Detection gaps over 3 hours for each fish were binned in four groups based on number of hours: 3-6, 6-12, 12-24, and > 24. The time of departure for all gaps over 6 hours was assessed using a Welch's ANOVA to see if long departures were unevenly spread throughout the day. A Tukey-Kramer HSD post hoc test was applied to see if any times were significantly greater than others.

Results

Departures over 6 hours were not spread evenly throughout the day ($F(23, 217.22) = 4.4442$, $p < 0.0001$) and departures 0500-0800 and 2000-2100 were more common ($p > 0.05$) than 1100-1300, 1500-1600 and 1700-1800. Daytime values 0800-2000 were below the average of .0417 while evening values tended to be above the average (with the exception of 0000-0100 and 2200-2300 which were below average) **(Figure A6).**

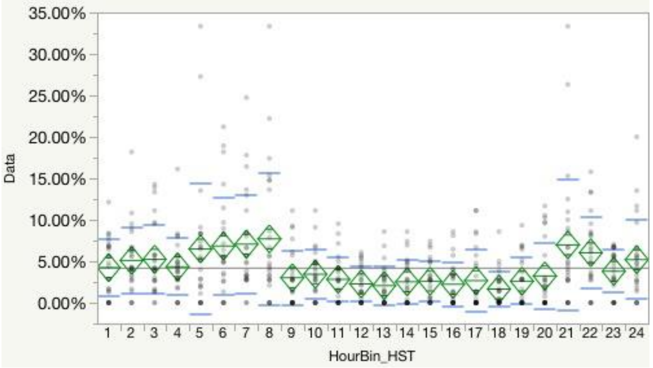


Figure A6: Gap start
Each point represents the percentage of gaps that occurred each hour for one fish. Blue bars are standard deviation. Green triangles show the mean and 95% confidence interval of the mean. The line at 4.17% indicates the expected value if gaps were spread evenly throughout the day.

Appendix-D: Supplementary discussion

Tag shedding

Apparent disappearance or death of fish could also be attributed to tag shedding. There have been numerous incidences of internally implanted tag expulsions from fish through the incision point, the body wall or intestine, all occurring with a low frequency of mortality. Ejection of tags can occur in 20-175 days and rates above 50% have been observed although the rate and process of ejection and is highly variable by relative size of the tag, environmental conditions such as temperature, and species with many species showing a shedding rate of zero (Jepsen 2002). We saw a sharp decline in residence ~50 days after being detected on the seamount and cannot rule out tag shedding as a contributing factor.

Survivability relates to fishing success

If we assumed fish not detected had died, we had much greater survival during the 2011 tag deployments than 2010 deployments. In contrast to the three 2010 cruises (during one of which no *E. illustris* were caught) the 2011 cruises had consistent landings of *E. illustris* and allowed more stringent selection of healthy individuals for tagging. Fish displaying less obvious signs of barotrauma were preferably chosen, and as a result survivability immediately after release increased from 20% in 2010 to 63% in 2011. The 2012 cruise, in which 33 fish were tagged and 11 (33%) tracked, had a combination of poor fishing for the majority of the trip and a single day at the end in which the majority of the tags were put out. This stresses the importance of good fishing and may limit the tagging species to fish that can be reliably caught in a healthy state or in enough numbers to find healthy ones to tag.

Appendix-E: Additional tables and figures

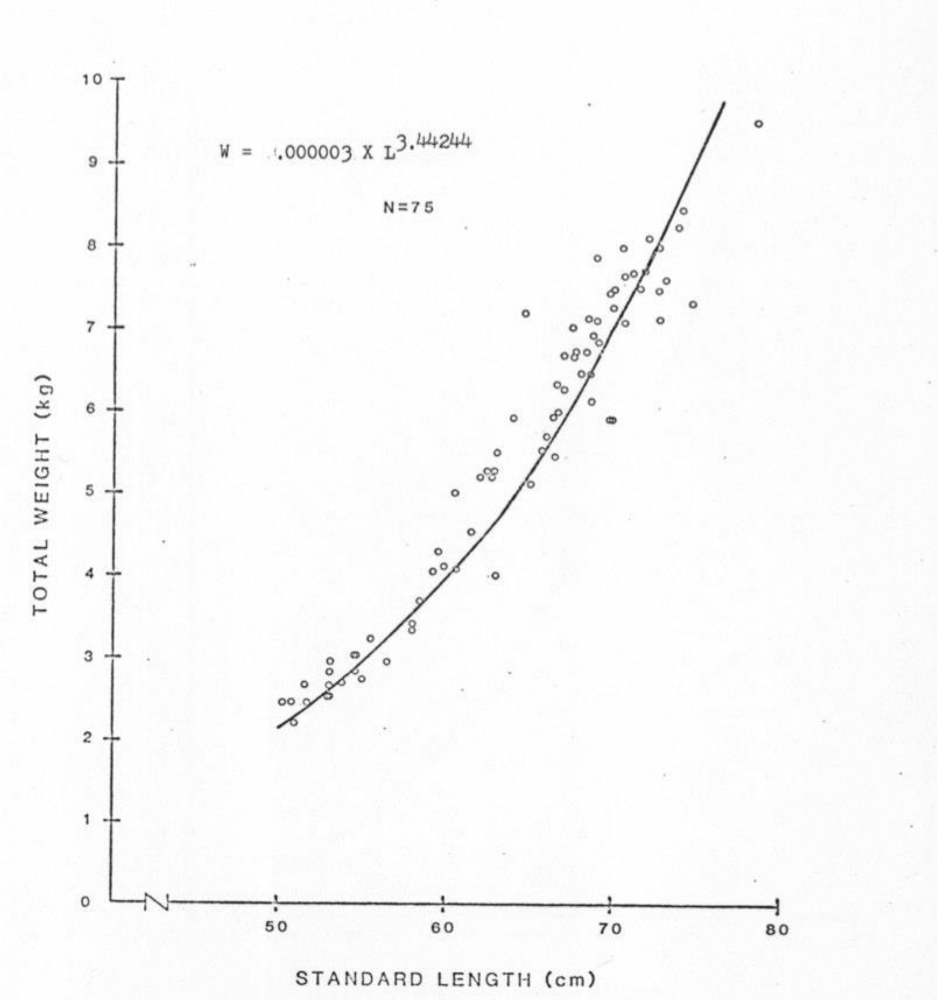


Figure E1: Length-weight curve for *E. illustris*
A length-weight curve was calculated as W=3*10-6*L3.44244 (Okamoto 1982)

Table E1: Gaps per day

Proportional time of gaps of different lengths for each fish. Gaps are binned into groups of <3 hours, 3-6 hours, 6-12 hours, 12-24 hours and >24 hours.

Fish ID	<3	3-6	6-12	12-24	>24
164	0.79	0.10	0.09	0.01	-
173	0.80	0.08	0.12	-	-
175	0.77	0.15	0.08	-	-
177	0.88	0.06	0.04	0.02	-
178	0.19	-	0.13	0.09	0.60
179	0.93	0.07	-	-	-
180	0.81	0.08	0.08	0.03	-
182	0.70	0.08	0.16	0.06	-
184	0.53	0.11	0.28	0.07	-
185	0.74	0.18	0.06	0.03	-
191	0.45	0.04	0.09	0.08	0.34
192	0.61	0.14	0.23	0.02	-
193	0.77	0.08	0.06	0.09	-
194	0.80	0.07	0.07	0.06	-
195	0.78	0.04	0.11	0.07	-
237	0.13	0.02	0.04	0.44	0.37
239	0.60	0.14	0.17	0.08	-
248	0.39	0.17	0.19	0.26	-
249	0.38	0.17	0.26	0.19	-
252	0.45	0.13	0.21	0.21	-
255	0.55	0.22	0.19	0.04	-
400	0.64	0.13	0.17	0.07	-
401	0.50	0.10	0.18	0.21	-
403	0.22	0.06	0.13	0.45	0.14
410	0.63	0.11	0.15	0.11	-
413	0.41	0.09	0.39	0.10	0.02

Appendix-F: Supplementary statistics tables

Table F1: Periodic detection rate Nonparametric Comparisons For All Pairs Using Steel-Dwass Method

Level	- Level	Score Mean Difference	Std Err Dif	Z	p-Value	Hodges-Lehmann	Lower CL	Upper CL
Night	Day	19.73077	4.203173	4.694255	<.0001*	6.693832	3.251568	9.878449
Night	Twilight	11.88462	4.203173	2.827534	0.0130*	4.307228	0.660854	8.064065
Twilight	Day	11.50000	4.203173	2.736028	0.0171*	1.822398	0.240211	3.501305

Table F2: Residency Index Nonparametric Comparisons For All Pairs Using Steel-Dwass Method

Level	- Level	Score Mean Diff	Std Err Dif	Z	p-Value	Hodges-Lehmann	Lower CL	Upper CL
Total	Southwest	25.0385	4.062483	6.16334	<.0001*	0.54	0.36	0.64
Total	East	24.0000	4.061184	5.90961	<.0001*	0.25	0.15	0.46
Middle	Southwest	23.5769	4.182399	5.63718	<.0001*	0.49	0.29	0.64
Total	North	19.0000	3.962684	4.79473	<.0001*	0.16	0.09	0.43
North	Southwest	15.1538	4.201558	3.60672	0.0029*	0.28	0.09	0.48
East	Southwest	12.1154	4.201558	2.88355	0.0321*	0.21	0.01	0.41
Total	Middle	9.2692	3.680285	2.51862	0.0865	0.01	0	0.04
East	North	-6.3077	4.200302	-1.50172	0.5613	-0.1	-0.23	0.1
North	Middle	-14.7692	4.150360	-3.55854	0.0034*	-0.15	-0.34	-0.03
East	Middle	-21.0000	4.181407	-5.02223	<.0001*	-0.24	-0.31	-0.13