A peer-reviewed version of this preprint was published in PeerJ on 6 September 2016.

<u>View the peer-reviewed version</u> (peerj.com/articles/2357), which is the preferred citable publication unless you specifically need to cite this preprint.

Jorgensen SJ, Klimley AP, Muhlia-Melo A, Morgan SG. 2016. Seasonal changes in fish assemblage structure at a shallow seamount in the Gulf of California. PeerJ 4:e2357 <u>https://doi.org/10.7717/peerj.2357</u>

Seasonal changes in fish assemblage structure at a shallow seamount in the Gulf of California

Salvador J Jorgensen Corresp., 1, 2, A. Peter Klimley 2 , Arturo Muhlia-Melo 3 , Steven G Morgan 4

¹ Conservation Research Department, Monterey Bay Aquarium, Monterey, California, United States

² Department of Wildlife, Fish, & Conservation Biology, University of California, Davis, Davis, California, United States

³ Department of Fisheries Ecology, Centro de Investigaciones Biológicas del Noroeste S. C., La Paz, Baja California Sur, Mexico

⁴ Bodega Marine Lab, University of California, Davis, Bodega Bay, California, United States

Corresponding Author: Salvador J Jorgensen Email address: sjorgensen@mbayaq.org

Seamounts have generally been identified as locations that can promote elevated productivity, biomass and predator biodiversity. These properties attract seamountassociated fisheries where elevated harvests can be obtained relative to surrounding areas. There exists large variation in the geological and oceanographic environment among the thousands of locations that fall within the broad definition of seamount. Global seamount surveys have revealed that not all seamounts are hotspots of biodiversity, and there remains a strong need to understand the mechanisms that underlie variation in species richness observed. We examined the process of fish species assembly at El Bajo Espiritu Santo (EBES) seamount in the Gulf of California over a five-year study period. To effectively guantify the relative abundance of fast-moving and schooling fishes in a 'blue water' habitat, we developed a simplified underwater visual census (UVC) methodology and analysis framework suitable for this setting and applicable to future studies in similar environments. We found correlations between seasonally changing community structure and variability in oceanographic conditions. Individual species responses to thermal habitat at EBES revealed three distinct assemblages, a 'summer assemblage' tracking warmer overall temperature, a 'winter assemblage' correlated with cooler temperature, and a 'year-round assemblage' with no significant response to temperature. Species richness was greatest in spring, when cool and warm water masses stratified the water column and a greater number of species from all three assemblages co-occurred. We discuss our findings in the context of potential mechanisms that could account for predator biodiversity at shallow seamounts.

Seasonal changes in fish assemblage structure at a shallow seamount in the Gulf of California Salvador J. Jorgensen^{a,b}, A. Peter Klimley^b, Arturo Muhlia-Melo^c, Steven G. Morgan^d ^aConservation Research Department, Monterey Bay Aquarium, 886 Cannery Row, Monterey, CA 93940, sjorgensen@mbayaq.org ^bDepartment of Wildlife, Fish and Conservation Biology, University of California, Davis, One Shields Avenue, CA 95616, USA, sjorgensen@mbayaq.org ^cDepartment of Fishereies Ecology, Centro de Investigaciones Biologicas del Baja California Sur, Apartado Postal 128, La Paz, Mexico, amuhlia04@cibnor.mx ^dBodega Marine Laboratory, P.O. Box 247 Bodega Bay, CA 94923, USA, sgmorgan@ucdavis.edu

24 Abstract.

25 Seamounts have generally been identified as locations that can promote elevated productivity, 26 biomass and predator biodiversity. These properties attract seamount-associated fisheries where 27 elevated harvests can be obtained relative to surrounding areas. There exists large variation in the 28 geological and oceanographic environment among the thousands of locations that fall within the 29 broad definition of seamount. Global seamount surveys have revealed that not all seamounts are 30 hotspots of biodiversity, and there remains a strong need to understand the mechanisms that 31 underlie variation in species richness observed. We examined the process of fish species 32 assembly at El Bajo Espiritu Santo (EBES) seamount in the Gulf of California over a five-year 33 study period. To effectively quantify the relative abundance of fast-moving and schooling fishes 34 in a 'blue water' habitat, we developed a simplified underwater visual census (UVC) 35 methodology and analysis framework suitable for this setting and applicable to future studies in similar environments. We found correlations between seasonally changing community structure 36 37 and variability in oceanographic conditions. Individual species responses to thermal habitat at 38 EBES revealed three distinct assemblages, a 'fall assemblage' tracking warmer overall 39 temperature, a 'spring assemblage' correlated with cooler temperature, and a 'year-round 40 assemblage' with no significant response to temperature. Species richness was greatest in 41 summer, when cool and warm water masses stratified the water column and a greater number of 42 species from all three assemblages co-occurred. We discuss our findings in the context of 43 potential mechanisms that could account for predator biodiversity at shallow seamounts.

45 Introduction.

46 Seamounts have long been identified as important ocean habitats with elevated predator 47 diversity (Hubbs, 1959; Morato et al., 2010a). Multi-species aggregations of fishes are 48 commonly reported at shallow seamounts (Klimley & Butler, 1988; Rogers, 1994; Morato & 49 Clark, 2007). These aggregations are targeted by numerous fisheries and data suggest that catch 50 rates for many fish species are higher near some seamounts relative to surrounding habitats 51 (Rogers, 1994; Genin, 2004; Morato et al., 2008). Shallow seamounts consist of relatively 52 shallow benthic habitat, within the euphotic zone, surrounded by adjacent deep-ocean (Lueck & 53 Mudge, 1997; Trasvina-Castro et al., 2003; Clark et al., 2010; Staudigel et al., 2010). Thus fishes 54 aggregating at these sites are demersal and reef-associated, as well as pelagic species common in 55 epipelagic environments (Holland & Grubbs, 2007; Litvinov, 2007; Morato & Clark, 2007; 56 Morato et al., 2008). However, seamounts are highly variable in their geologic and 57 oceanographic characteristics, and not all seamounts have fish aggregating properties (Kvile et 58 al., 2014). Among the potential mechanisms and drivers, examining the oceanographic 59 conditions promoting seamount productivity, predator aggregation, and species richness remains 60 an important research gap (Clark et al., 2012; McClain & Lundsten, 2015; Morato et al., 2015). 61 Tracking seamount community assembly over time in relation to natural oceanographic 62 variability can provide unique insights into seamount ecology.

63

64 The mechanisms for why fishes sometimes occur in higher densities at shallow
65 seamounts fall into two general categories. First, some seamounts may provide elevated foraging
66 opportunities. Trophic subsidies likely result as seamounts generate conditions such as increased
67 vertical nutrient fluxes and plankton retention that increase productivity and fuel higher trophic
68 levels (Lueck & Mudge, 1997; Genin, 2004). Second, seamounts may provide spatial reference

points or refugia for migratory species (Klimley, 1993; Freon & Dagorn, 2000). However, the
processes that determine the composition of fish species and elevated predator richness have
received comparatively little attention, and remain uncertain (McClain, 2007; Morato et al.,
2010a).

73

74 One hypothesis for increased fish species richness at seamounts is the enhanced 75 availability of limiting trophic resources (Worm, Lotze & Myers, 2003; McClain, 2007; Morato 76 et al., 2010a). This idea is essentially an extension of the 'species-energy' hypothesis (Wright, 77 1983), which predicts that the diversity of one trophic level is determined by the amount of 78 energy available from the level below. If elevated forage availability at seamounts supports a 79 greater number of individuals and, in turn, species richness, then food should be the primary 80 resource of interest for fishes that visit seamounts, and more visitors (species) should occur when 81 food supply is elevated.

82

83 An alternative hypothesis is that seamounts comprise diverse and heterogeneous habitats, 84 which provide a variety of resources and environmental conditions suitable for a range of fish 85 species and life history functions. The 'habitat heterogeneity' hypothesis is a long-standing tenet 86 of terrestrial ecology (e.g. Simpson, 1949; MacArthur & Wilson, 1967; Tews et al. 2004) 87 whereby structurally complex habitats may provide more ways of exploiting environmental 88 resources and thereby increase species diversity. Under this hypothesis more species are 89 predicted to co-occur when habitat is more complex, or when the breadth of resources exploited 90 increases.

91

92 To explore processes of seamount community assembly and variation in fish species 93 richness we tracked the relative abundance of conspicuous shallow seamount-associated fish 94 species at El Bajo Espiritu Santo (EBES) seamount over a five-year period. To overcome the

95 difficulty in quantifying relative abundance for fast-moving and schooling fishes in a 'blue 96 water' habitat, we developed a simplified underwater visual census (UVC) methodology and 97 analysis framework suitable for this setting and applicable to future studies in similar 98 environments. We compared the results of UVCs and experimental fishing surveys over time 99 with oceanographic parameters to determine how changes in seamount community structure 100 correlated with natural environmental variability. We discuss the results in the context of two 101 hypotheses, 'species-energy' and 'habitat heterogeneity' as they relate to seamounts as predator 102 diversity hotspots.

103

104 Methods.

105 Study area

106 El Bajo Espiritu Santo Seamount (EBES) is located in the lower Gulf of California 107 (24°42'N, 110°18'W) 56 km north of La Paz (Fig. 1a). The summit of the seamount reaches a 108 minimum depth of 18m and drops off to between approximately 500 and 1000 m on all sides (for 109 detailed bathymetric view see Fig. 1 in Klimley, 1993). The upper part of the seamount, within 110 30 m of the surface, forms a broad ridge that is approximately 500 m long and 100 m wide. 111 Numerous demersal, reef-associated and pelagic fish species inhabited the water column between 112 this ridge and the water surface, and this seamount-associated community was the focus our 113 study.

114

115 Underwater visual censuses

We conducted underwater visual censuses (UVCs) at EBES from 1999 to 2004 by
measuring encounter rates for individuals of 27 conspicuous predator and prey fish species
(Table 1) along transects using SCUBA. Divers recorded the identity and number of individuals

119 of each target species encountered on a waterproof slate. Data were consistently collected by the 120 same few divers throughout the study. Transects were initiated at random starting points near one 121 end of the seamount ridge and proceeded on a compass bearing along its length in either a 122 northwesterly or southeasterly direction. If currents were too strong to swim against, the census 123 was initiated at a random starting point near the up-current end of the ridge, allowing divers to 124 drift with the current. Censuses proceeded for 40 minutes while divers swam toward a constant 125 compass bearing at a relatively constant speed of approximately 0.2 ms⁻¹. In order to sample 126 across all depths between 0 and 30 m while maintaining safe SCUBA protocols, divers began 127 sampling immediately upon leaving the surface while gradually descending. Once the maximum 128 depth was reached (25 to 30 m), divers began a very gradual ascent with a goal of reaching the 129 surface at the 40 minute mark. Fish were only counted if they appeared within 5 m of the 130 observer in any direction forward of a plane perpendicular to the swimming direction. Visibility 131 was estimated by divers from the difference between the depth of the seamount substrate and the 132 depth at which this substrate first became visible as the diver descended toward it. Visibility was 133 measured only when a light patch of sand near the seamount summit (20 m) was not visible from 134 the boat at the surface. During censuses, visibility ranged from 7 m to > 20 m.

Among species, considerable variability occurred in the number of individuals encountered per observation. For example, green jacks (*C. caballus*) often occurred in large schools (n > 128) when present at the seamount, while yellowtail (*S. lalandi*) counts seldom exceeded 12 individuals per transect. Additionally, several species were generally either absent from the seamount or present in large numbers. To minimize bias and sampling error, we organized our counts into classes or ''bins' with central values expressed on a log² scale, i.e. centers 0 and 2^{*i*} where *i* = 0-7. For example 2⁰ denotes a count of one individual, 2¹ represents a

class of between 1.4 and 2.8 individuals $(2^{0.5} - 2^{1.5})$ with a central value of 2, and 2^2 refers to a 142 class of 2.9 - 5.6 individuals $(2^{1.5}-2^{2.5})$ with a central value of four, and so forth (Table 2). Thus, 143 144 bin width expanded exponentially with the number of individuals counted assuring that even 145 large numbers of rapidly moving fish could be accurately estimated to be within one of the range 146 categories. When the number of individuals was too large or difficult to count accurately during 147 censuses, the number was estimated to the nearest central value and corresponding ordinal score. 148 This procedure provided an objective criterion for quickly sorting raw counts into a number of 149 ordinal categories. Additionally this procedure resulted in a log-transformation of the data, 150 thereby increasing the 'spread' and resolution for species with lower counts (see Tables 2 and 3) 151

152 Fishing surveys

After each census, we conducted standardized fishing surveys to detect species that were less frequently encountered while using SCUBA. We recorded captures (presence or absence) of *Thunnus albacares, Corphaena hippurus,* and *Acanthicybium solanrdi* during 60-min fishing periods. Our tackle consisted of monofilament line that was attached directly to a hook, and baited with a single herring, *Harengula thrissina*. Three of these 20-m long rigs were deployed simultaneously while the boat drifted over the seamount. Ethical review was not required for sampling of marine fishes in fishing surveys.

160

161 Environmental records

At EBES, we recorded daily water temperature at a depth of 30 m using an in situ temperature logger (Onset Corporation, Tidbit Stowaway, and Water Temp Pro). Sea surface temperature (SST14NA) was downloaded from the National Environmental Satellite, Data, and

165 Information Service (NESDIS) online database (www.class.noaa.gov). This SST14NA product 166 was generated every 48 hours and referenced to in situ measurements at 1 m depth. Temperature profile were obtained opportunistically from casts taken at points along SW-NE transects that 167 168 bisected EBES (Trasvina-Castro et al., 2003) on November 24, 1997, September 10, 1998, and June 22, 1999. Data collected \leq 5 km from the seamount (n = 4 - 7) were partitioned into depth 169 170 bins and averaged for each date. A fourth temperature/depth profile was acquired from a data 171 archiving tag (Wildlife Computers Inc., PAT), which was attached to a shark (Sphyrna lewini) at 172 EBES. Minimum and maximum temperatures were recorded from seven depths (4, 16, 100, 156, 173 260, 316, and 368 m) as the shark swam through the water column shortly after tagging on 174 February 2, 2004. These data were later transmitted from the tag via satellite after the tag 175 released from the shark (Jorgensen, Klimley & Muhlia-Melo, 2009).

176

177 Analysis

178 Censuses were conducted at irregular intervals over the duration of the study period. Each 179 independent observation was recorded as the mean value of replicate censuses (n = 1-4) that 180 were completed within a calendar month. The mean number of encounters per transect for each 181 species was then given an ordinal score following the \log_2 classification scheme (see table 2). To 182 examine the influence of seasonal oceanographic processes on the relative abundance of pelagic 183 species at EBES, we used multiple logistic regression analysis (SAS Institute Inc., JMP). Of 27 184 species observed at the seamount, we considered only those present in > 10% of census 185 observations (n = 17 species) for analysis. Ordinal score was regressed over monthly mean SST 186 and monthly mean water temperature at 30 m depth (T30). We used the same technique for 187 analyzing our fishing survey data, except the dependent variable was binary (presence and

absence) rather than ordinal. To verify the assumption of temporal independence among observations, we performed time series analysis on the regression residuals. There was no significant autocorrelation at any lag time for any species ($\alpha = \pm 2$ SE). T30 measurements were not collected during three months, October 2003, May 2004, and June 2004, and a value was estimated for these months by averaging temperatures of the respective months collected during all other years (n = 5 - 6).

194

195 To further understand temporal patterns in the co-occurrence of seamount species we 196 plotted species abundance curves over time. This qualitative gradient analysis facilitated 197 visualizing the seasonal separation and overlap of species at the seamount. We summarized 198 census data from all five years into a single seasonal cycle (12 months) by taking the mean of all 199 the census scores for each species by month, then normalizing by the highest value, so that 200 relative abundance could be compared among species. We then fit a curve though the monthly 201 values for each species using locally weighted smoothing via least squares quadratic polynomial 202 fitting (Loess fit; MatlabTM, Mathworks).

203

To compare the number of species present at the seamount with sea temperature, the presence or absence of the 17 species was summarized by month. A species was scored as present if it was observed during that month in any year during the study. An index of species richness for each month was determined as the sum of the number of target species that were present. The temperature gradient near the surface (SST - T30) during each month was calculated as the mean difference between SST and T30 over all years. We used standard linear

- 210 regression analysis to determine whether there was a significant correlation between the number
- 211 of species observed and SST, T30, or near-surface temperature gradient.
- 212
- 213 Results.
- 214 Oceanographic environment

215 The seamount environment was characterized by substantial variation in temperature both 216 temporally and in terms of vertical thermal gradient. However, the annual cyclic pattern was 217 relatively predictable. Between 1999 and 2005 the mean 2-day Sea Surface Temperature at 218 EBES was 24.4°C and ranged from 18.3 to 32.5 °C (Fig. 1B). Sea surface temperature generally 219 peaked near 32 °C in August and September then decreased rapidly from October through 220 January to a low near 19 °C in February and March. Throughout summer, STT increased steadily 221 but gradually. Mean daily T30 was 21.8 °C and ranged from 16.1 to 29.8 °C with maxima during 222 September and October and minima from January to June. Colder deep water persisted during 223 the spring and early summer as surface temperatures warmed, resulting in a strong and shallow 224 thermocline that lasted through July. T30 then typically rose sharply to its yearly high peak. By 225 November both SST and T30 typically fell rapidly as mixing deepened.

226

227 Periodic temperature profile measurements at EBES revealed the extent of seasonal 228 changes throughout the water column. Most annual variability occurred above 200 m (Fig. 2). 229 Temperature was relatively constant (\sim 13°C) at 200 m depth but there were considerable 230 differences in the depth of the mixed layer and the degree of stratification in the upper near-231 surface layer. Although SSTs were similar in June and November (\sim 27°C) the temperature cast 232 from June 1999 revealed strong stratification with a gradient of > 8°C in the top 30 m. This

observation is consistent with the average observed difference between mean SST and T30 in June (mean = 8.4), as shown by the difference between the gray line and dark line each June in Fig. 1c. The cast from November revealed a deep mixed layer extending to \sim 70 m. This deep mixing generally persisted through December.

- 237
- 238 Censuses

239 A total of 53 individual census dives were conducted at irregular intervals over 62 months from May 1999 to Aug 2004. These were averaged by calendar month resulting in 26 240 241 independent observations over the study period (Table 3). The relative abundance of species 242 encountered during censuses at EBES at different times of the year revealed changes in the 243 community structure. For many species, a clear seasonal signal was evident when relative 244 abundance was plotted over time against SST and T30. For example, Seriola lalandi was generally absent from the seamount during warm seasons, but generally peaked in abundance 245 from January to April, when temperatures were low (~20°C; Fig. 3A). In contrast, peaks in 246 247 Lutjanus novemfasciatus abundance coincided with positive peaks in SST and T30 between 248 August and November when temperatures were high (~ 27 and 32° C respectively; Fig. 3b). 249

Sea surface temperature and T30 were both significant predictors (multiple logistic regression, P < 0.05) of seasonal relative abundance for eight species (Table S1). There was also a significant nominal (presence or absence) response (P < 0.05) to STT and T30 for *C. hippurus*, based on fishing surveys (Table S1). To better understand the differing responses to oceanographic cycles by community members, we used the coefficients of the two regressors (β_{SST} and β_{T30}) as ordination axes and plotted each species in relation to these environmental

256 gradients (Fig. 4; Table S1). For negative log-likelihood, a negative β values along either axis 257 denotes a positive effect, and a positive β value indicates the opposite. Therefore, higher positive 258 values for a combination of β_{SST} and β_{T30} values indicated a greater affinity with colder sea 259 temperatures, and vice versa. The species fell into one of two groups divided by a line separating 260 warm and cold affinity with slope = -1, and intercepts (0, 0), and we categorized individuals as 261 cold or warm associated community members accordingly. 262 263 The cold associated group consisted of L. peru, S. lalandi, S. revoliana, and M. jordani. 264 The warm associated group consisted of C. caballus, C. hippurus, L. argentriventris, L. 265 novemfasciatus and S. lewini. A third group was represented year-round, as indicated by a non-266 significant negative log likelihood (P > 0.05). These species consisted of A. solandri, D. 267 macarellus, E. lineatus, H.guntherii, L. colorado) M. rosacea, P. colonus, and T. albacares. The 268 composition of species at EBES clearly differed seasonally, and we refer to three distinctive groups as the 'spring assemblage' (cold), 'fall assemblage' (warm), and 'year-round assemblage' 269 270 (no significant response to temperature). We refer collectively to all three groups as the 271 seamount-associated community. 272

273 Species curves

To better visualize the seasonal process of species turnover we plotted species seasonal distribution curves (Fig. 5). The resulting curves indicate strong temporal partitioning among the fall and spring assemblages, with some overlap near the distribution tails at the boundaries that occurred during December through February and May through July (Fig. 5A and B). Within assemblages the curves were somewhat offset, but more similar within the spring assemblage

279 than the fall. Abundance was near zero during warm months for all four spring species (also see 280 Table 4), and the seasonal peaks where more aligned except that S. lalandi was shifted slightly 281 earlier than the others. Among fall assemblage members, abundance curves did not overlap as 282 clearly. Some members were absent altogether from the seamount during the colder months, 283 while others were still present in low numbers. For example, C. caballus and C. hippurus were 284 never observed in winter months between January through April and May respectively, while L. 285 argentriventris was observed during every month of the year, but peaked in abundance during the warmer periods (see Table 4). Within the year-round assemblage abundance curves were 286 287 generally less defined in amplitude and peaked at different times (Fig. 5C). Some notable 288 exceptions include L. Colorado and A. solandri whose curves resemble those of the fall 289 assemblage, and *M. rosacea*, which resembled the spring assemblage.

290

291 Variation in species richness

The pattern of seasonal species turnover lead to variation in the cumulative number species observed during each month (min = 8 and max = 16 species). There was a positive linear relationship (p = 0.004) between the number of species and the surface to 30 m thermal gradient (Fig. 6). There was no significant relationship found between number of species and SST (p =0.139) or T30 (p = 0.921). More species were observed when members of all assemblages overlapped from June through August, a season when greater thermal heterogeneity, warm surface and cool deep water (\geq 30m), characterized the seamount environment (see Fig 1c).

301 Discussion.

302 Underwater visual censuses are particularly challenging in open water where large 303 schools of rapidly swimming individuals need to be quantified and recorded. The method of log 304 scale ordinal bins presented here provides a simple and accurate way to estimate relative 305 abundance where precision is scaled inversely with sampling difficulty to minimize observer 306 error. The resulting ordinal binning is appropriate for logistic regression; a robust multivariate 307 approach relevant to zero-inflated datasets. The resulting patterns of variation in the composition 308 and number of species provided insights relevant to the processes of shallow seamount fish 309 assemblage. Although the study was confined to a single seamount, the patterns observed over a 310 five-year period were clear and can be evaluated in the context of potential hypotheses 311 explaining elevated predator richness at seamounts. 312 313 Functional similarities in distinct fish assemblages 314 For species that were present year-round, the seamount environment likely fulfills 315 multiple vital life-history functions, including feeding, refuge, and reproduction. However, what 316 specific function does the seamount provide for the spring and fall assemblages? The arrival of 317 certain community members at EBES coincided with reported months of spawning aggregations 318 in the Gulf of California. These included members of both the fall and spring groups. L. 319 novemfasciatus generally peaked at EBES near September (see Fig. 3B), which is the reported 320 spawning season for this species in the Gulf of California (Sala et al., 2003). Apart from these 321 peaks in abundance, L. novemfasciatus generally was absent from EBES. Sala et al. (2003) also 322 reported S. lalandi aggregations spawning at reefs and seamounts in April, citing observations of

323 high densities and hydrated eggs in gonads. Peak abundance of S. lalandi at EBES occurred

324 between January and April (see Fig. 3A). All three female S. lalandi sacrificially sampled in the 325 fishing surveys at EBES during a large aggregation on February 3, 2003 had large gonads with 326 hydrated eggs. A single male captured during this event released milt as it was brought aboard. 327 Thus the arrival of L. novemfasciatus and S. lalandi at EBES, although during opposite seasons, were both linked to yearly spawning (Sala et al., 2003). Migrations to site and season-specific 328 329 spawning aggregations, can be on the order of hundreds of kilometers (Bolden, 2000), could 330 potentially be to find conspecifics or to select environmental conditions favoring larval survival 331 (Johannes 1978).

332

333 Like many seamounts, EBES is a distinct geophysical feature, and is likely to function as 334 a navigational (reference) or meeting (destination) point where wide-ranging organisms come 335 together for mating events or otherwise. Sphyrna lewini, a member of the fall assemblage, 336 aggregates in large groups at EBES and other seamounts (Klimley & Nelson, 1984). Previous 337 studies have illustrated their emigration, alone or in small groups, away from EBES to 338 surrounding open waters at night, presumably to forage, and return to the seamount the following 339 dawn (Klimley & Nelson, 1984; Klimley, 1993). While foraging and mating apparently do not 340 occur at EBES, during the day, the dense schools of hammerhead sharks remained closely 341 associated with EBES slowly swimming back and forth along the ridge. Thus seamounts appear 342 to provide a refuge and spatial reference.

343

Enriched foraging potential at shallow seamounts is another potential attraction for visitors and may increase their residence time. (Fontenau, 1991) suggested that certain seamounts may enhance foraging by *T. albacares*, and some, but not all seamounts are associated with increased

347 catch per unit effort of *T. albacares* and other tuna species (Morato et al., 2010b). At EBES 348 schools of T. albacares were frequently observed feeding (personal observation). Individual 349 tunas tagged with acoustic tags remained resident near EBES at all times of the year for periods 350 ranging from a few days to greater than a year (Klimley et al., 2003). During prolonged 351 residence, the intervals between detections were brief and indicated the tunas could rarely have 352 moved more than 900 m from EBES. While not all tagged T. albacares resided at the seamount, 353 those that did likely foraged in close association with EBES over extended periods. In addition to 354 foraging, seamounts also may play a role in navigation for T. albacares (Holland, Kleiber & 355 Kajiura, 1999), which could explain why some tuna remained resident while others did not 356 (Klimley et al., 2003).

357

From these observations of just some of the assemblage members, it seems clear that pelagic and reef-associated fishes (see Table 1) co-occur at EBES to fulfill a variety of functions including foraging, spawning and navigation. These and possibly other drivers attracted seamount visitors during a range of seasonally varying environmental conditions. There was a large range in the overall temperature and water column thermal structure (Figs. 1 and 2). Yet spawning, foraging, and navigation occurred at various times throughout the year (e.g. spawning by fall and spring assemblage members) despite the contrasting environmental conditions.

365

366 Assemblage cohesion

Our data reveal how local seamount communities are ephemeral and structurally
dependent on seasonal and regional oceanographic conditions. At EBES distinct assemblages
were evident associated with pronounced seasonal changes in oceanography. Many pelagic fish
species, such as tunas, track thermal fronts and other oceanographic features (Laurs, Yuen &

Johnson, 1977; Kitagawa et al., 2007; Schaefer, Fuller & Block, 2007) and reside for extended
periods around seamounts (Holland, Kleiber & Kajiura, 1999; Klimley et al., 2003). Thus, the
movement of oceanographic features over seamounts may determine the pool of species
available at a given time and the composition of seamount-associated communities.

375

376 (Klimley & Butler, 1988) hypothesized that some fish species groups may occur as 377 'mobile communities' in the open ocean arriving and departing from local seamounts as a single 378 unit. We were unable to track the precise arrival and departure timing of assemblage members, 379 however, a number of results suggest that members converged at EBES under slightly different 380 conditions, and for different purposes. Ordination analysis clearly grouped overall warm 381 associated species distinctly from the cold associated group (see Fig. 4). Within these groups, 382 however, further structure was evident. For example, in the fall assemblage, C. caballus 383 abundance was highly correlated with warmer SST, but also negatively correlated with T30 (Fig 384 4: Table S1): conditions that prevail in summer. In contrast S. lewini abundance was highly 385 positively correlated with warmer T30, but negatively correlated with warmer SST (Fig. 4; Table S1); typical fall conditions (Figs. 1 and 2). This structure was further evident in the offset of 386 387 abundance curve peaks between C. caballus in August, and S. lewini in November (Fig. 5a). The 388 remaining fall assemblage members peaked in abundance somewhere between these two (Figs. 4 389 and 5). Similar structure, although more subtle, occurred for the spring assemblage.

390

This general offset in peak relative abundance suggests that members likely did not arrive together. Furthermore, within the fall assemblage, some species were present at EBES in low abundance year-round during the off-peak seasons (e.g. *L. argentiventris*) while others were completely absent when not in peak abundance (e.g. *C. caballus*). Finally, within-assemblage differences in the nature of each species association with the seamount (e.g. *L. novemfasciatus* gathered to spawn, while *S. lewini* aggregated at EBES during daylight and foraged away at

night) suggest that at least some members co-occurred at the seamount for dissimilar reasons.
We conclude that assembly of seamount community members at EBES was largely the result of
'species-individualistic' processes. The associations between aggregating species were
seasonally ephemeral, and likely confined to this place and time. Once aggregated at the
seamount, however, it seems possible that sudden movements of water masses, on short time
scales, might influence an entire assemblage, away from or back to a seamount (Klimley &
Butler, 1988).

404

405 Species richness

406 Water temperature is a strong predictor for species richness among broad marine taxa; for 407 open ocean fishes and foraminifera this convex function peaks near 25° C (Rutherford, D'Hondt 408 & Prell, 1999; Worm et al., 2005; Whitehead, McGill & Worm, 2008) and at corresponding 409 intermediate latitudes (Morato et al., 2010a). The mean SST at EBES was 25.4° C and ranged seasonally from 18 to 30° C. Given the movement potential of the seamount-associated species 410 411 and the prevalence of seasonally advancing and retreating thermal fronts ((Klimley & Butler, 412 1988; Trasvina-Castro et al., 2003; Douglas et al., 2007); Fig. 1), one might predict that the greatest number of species would occur at EBES when temperature were near 25° C. A mean 413 414 SST of 25° C occurred twice each year at EBES; during summer (May) and late fall (November) 415 transitions respectively (Fig. 1). However, increased predator richness at the seamount was not 416 predictable by surface temperature alone. Instead, it was correlated with greater vertical thermal 417 gradient. Interestingly, the strongest gradients occurred in summer and the weakest in late fall. In essence increased species richness did occur when surface temperature was near 25° C, but only 418 419 during summer when processes occurring below the surface where the likely drivers.

421 The early summer peak in total species numbers at EBES was largely a transition period 422 after the average peak in abundance of the spring assemblage (March) and before that of the fall 423 assemblage (September); apparently not the prime 'target' period for either group. That species 424 co-occurred for a number of different functions also suggests that it was not linked to a single 425 prevalent environmental state. In fact the highest variability in temperature, both temporally and 426 spatially (i.e. in the water column), occurred then, suggesting increased habitat heterogeneity 427 itself is likely to be an important factor. Summer is a warming transition period at EBES when 428 warm and cold water occurs simultaneously providing a thermally heterogeneous habitat. This 429 range of temperatures, accessible across a narrow range of depths, may accommodate the 430 thermal optima (Blank et al., 2002; Boyce, Tittensor & Worm, 2008) of a wider range of species 431 thereby enabling the co-occurrence of both fall and spring assemblages. Globally, over broad 432 spatial and temporal scales, pelagic tuna and billfish diversity positively correlates with spatial 433 temperature (SST) gradient, and where data are available, tuna and billfish diversity correlates in 434 turn with total predator diversity (Worm et al., 2005).

435

Our results suggest that increased habitat heterogeneity through vertical and temporal thermal gradients may be an important mechanism for increased species richness at the local scale and may also shape patterns of diversity of vagile ocean fishes at larger scales. The turnover of species at EBES, or 'beta diversity', was clearly reflected through time with changes in temperature. In turn these species co-occurred (overlapped) when a wide range of thermal habitat was available.

443 In addition to habitat heterogeneity, a potential alternative explanation is that enhanced 444 foraging opportunities may increase species richness via the 'species-energy' hypothesis (Worm, 445 Lotze & Myers, 2003; McClain, 2007; Morato et al., 2010a). What can seasonal variation at 446 EBES tell us about a trophic link to observed changes in species richness? Local food supply 447 could be augmented, either through vertical mixing and elevated primary productivity, or 448 through concentration of macroplankton (Wolanski & Hamner, 1988; Genin, 2004). It is unlikely 449 that the residence time of upwelled water around seamounts is sufficiently long for primary 450 production enrichment to propagate up the food web to the level of predatory fishes (Genin, 451 2004). However, a match between enhanced primary productivity and early life-history survival 452 (Cushing, 1990) could increase larvae fitness for fishes spawning at seamounts whether water 453 masses (including nascent larvae) were advected or retained. That at least two species aggregated 454 at EBES to spawn suggests enhanced primary production at seamounts could be one mechanism 455 for increasing predator fish richness that is not directly related to the 'species-energy' model. 456

457 Primary productivity in the Gulf of California is typically highest during fall/winter, 458 when strong winds drive regional upwelling, and lowest in spring/summer (Douglas et al., 2007). 459 However, another important mechanism for primary productivity in the Gulf is tidally driven 460 vertical mixing (Trasvina-Castro et al., 2003; Douglas et al., 2007). At EBES dynamic instability 461 and mixing due to vertical current sheer occur over the top of the seamount (Trasvina-Castro et 462 al., 2003; Douglas et al., 2007). Vertical mixing at this depth would likely be drowned out in 463 fall/winter when the mixed layer typically extends well below 50 m (Fig. 2) but may become 464 locally important during spring/summer when the thermocline is shallow and wind driven 465 production is regionally limiting.

466

467 The most widely accepted mechanism for enhanced foraging at seamounts involves a 468 biophysical match between currents and animal behavior (Genin, 2004; McClain, 2007). 469 However, quantifying prey (zooplankton) availability was beyond the scope of this study. While 470 this mechanism cannot therefore be directly addressed as a contributing factor for increased 471 richness, two observations suggest it may not be the primary driver at EBES. First, many species 472 arrived at the seamount for reasons other than foraging. Second, the summer period, when the greatest number of species was observed, appeared to be a 'transition' period rather than a 473 474 'target' period for either fall or spring assemblages. If foraging were the primary common driver 475 explaining increased richness during summer, then one might expect more species to coincide in 476 their peak abundance.

477

Ultimately these observations are also more consistent with the 'habitat heterogeneity' 478 479 hypothesis since fish species occurred at EBES for a variety of functions including foraging, 480 spatial reference and reproduction during different seasons. The intra-annual turnover of species, 481 or temporal beta-diversity resulted in seasonal variation in fish species numbers at EBES that 482 was positively correlated with thermal heterogeneity in the water column. Although this study 483 was limited to a single seamount location, the UVC methods and clear patterns observed enable 484 comparisons to other locations, and in this case provide support for the idea that 485 oceanographically heterogeneous and dynamic seamounts may support greater predator richness. 486

487 Acknowledgements.

488 Considerable logistical support was provided by H. Fastenau, L. Inman, F. McLeese, M.
489 Cota, J. Richert, J. Downs, I. Nevius, M. Silva, numerous staff of Centro de Invesigaciones

- 490 Biologicas del Baja Norte of La Paz, and the Cortez Club. We also thank C. Logan for helpful
- 491 review and comments on the manuscript.
- 492
- 493

494 **References.**

496	Blank J., Morrissette J., Davie P., Block B. 2002. Effects of temperature, epinephrine and Ca2+
497	on the hearts of yellowfin tuna (Thunnus albacares). Journal of Experimental Biology
498	205:1881–1888.
499	Bolden S. 2000. Long-distance movement of a Nassau grouper (Epinephelus striatus) to a
500	spawning aggregation in the central Bahamas. Fishery Bulletin 98:642-645.
501	Boyce DG., Tittensor DP., Worm B. 2008. Effects of temperature on global patterns of tuna and
502	billfish richness. Marine Ecology Progress Series 355:267–276. DOI:
503	10.3354/meps07237.
504	Clark MR., Rowden AA., Schlacher T., Williams A., Consalvey M., Stocks KI., Rogers AD.,
505	O'Hara TD., White M., Shank TM., Hall-Spencer JM. 2010. The Ecology of Seamounts:
506	Structure, Function, and Human Impacts. Annual Review of Marine Science 2:253–278.
507	DOI: 10.1146/annurev-marine-120308-081109.
508	Clark MR., Schlacher TA., Rowden AA., Stocks KI., Consalvey M. 2012. Science Priorities for
509	Seamounts: Research Links to Conservation and Management. PLOS ONE 7:e29232.
510	DOI: 10.1371/journal.pone.0029232.
511	Cushing D. 1990. Plankton production and year-class strength in fish populations - an update of
512	the match mismatch hypothesis. Advances in Marine Biology 26:249–293.
513	Douglas R., Gonzalez-Yajimovich O., Ledesma-Vazquez J., Staines-Urias F. 2007. Climate
514	forcing, primary production and the distribution of Holocene biogenic sediments in the
515	Gulf of California. Quartenary Science Reviews 26:115-129. DOI:
516	10.1016/j.quascirev.2006.05.003.

517	Fontenau A. 1991. Seamounts and tuna in the tropical Atlantic. Aquatic Living Resources 4:13-
518	25.
519	Freon P., Dagorn L. 2000. Review of fish associative behaviour: toward a generalisation of the
520	meeting point hypothesis. Reviews in Fish Biology and Fishes 10:183–207.
521	Genin A. 2004. Bio-physical coupling in the formation of zooplankton and fish aggregations
522	over abrupt topographies. Journal of Marine Systems 50:3-20. DOI:
523	10.1016/j.marsys.2003.10.008.
524	Holland KN., Grubbs RD. 2007. Fish Visitors to Seamounts: Tunas and Bill Fish at Seamounts.
525	In: Pitcher TJ, Morato T, Hart PJB, Clark lcolm R, Haggan N, Santos RS eds.
526	Seamounts: Ecology, Fisheries & Conservation. Blackwell Publishing Ltd, 189–201.
527	Holland KN., Kleiber P., Kajiura SM. 1999. Different residence times of yellowfin tuna,
528	Thunnus albacares, and bigeye tuna, T-obesus, found in mixed aggregations over a
529	seamount. Fishery Bulletin 97:392–395.
530	Hubbs CL. 1959. Initial Discoveries of Fish Faunas on Seamounts and Offshore Banks in the
531	Eastern Pacific.
532	Jorgensen SJ., Klimley AP., Muhlia-Melo AF. 2009. Scalloped hammerhead shark Sphyrna
533	lewini, utilizes deep-water, hypoxic zone in the Gulf of California. Journal of Fish
534	Biology 74:1682–1687. DOI: 10.1111/j.1095-8649.2009.02230.x.
535	Kitagawa T., Boustany A., Farwell C., Williams T., Castleton M., Block B. 2007. Horizontal and
536	vertical movements of juvenile bluefin tuna (Thunnus orientalis) in relation to seasons
537	and oceanographic conditions in the eastern Pacific Ocean. Fisheries Oceanography
538	16:409–421. DOI: 10.1111/j.1365-2419.2007.00441.x.

539	Klimley AP. 1993. Highly Directional Swimming by Scalloped Hammerhead Sharks, Sphyrna
540	lewini, and Subsurface Irradiance, Temperature, Bathymetry, and Geomagnetic-Field.
541	Marine Biology 117:1–22.
542	Klimley AP., Jorgensen SJ., Muhlia-Melo A., Beavers SC. 2003. The occurrence of yellowfin
543	tuna (Thunnus albacares) at Espiritu Santo Seamount in the Gulf of California. Fishery
544	Bulletin 101:684–692.
545	Klimley AP., Butler S. 1988. Immigration and emigration of a pelagic fish assemblage to
546	seamounts in the Gulf of California related to water mass movements using satellite
547	imagery. Marine Ecology-Progress Series 49:11-20.
548	Klimley AP., Nelson DR. 1984. Diel movement patterns of the scalloped hammerhead shark
549	(Sphyrna lewini) in relation to El Bajo Espiritu Santo: a refuging central-position social
550	system. Behavioral Ecology and Sociobiology 15:45–54.
551	Kvile KØ., Taranto GH., Pitcher TJ., Morato T. 2014. A global assessment of seamount
552	ecosystems knowledge using an ecosystem evaluation framework. Biological
553	Conservation 173:108-120. DOI: 10.1016/j.biocon.2013.10.002.
554	Laurs RM., Yuen HSH., Johnson JH. 1977. Small-scale movements of albacore, Thunnus
555	alalunga, in relation to ocean features as indicated by ultrasonic tracking and
556	oceanographic sampling. Fishery Bulletin 75(2)1607:347-355.
557	Litvinov F. 2007. Fish Visitors to Seamounts: Aggregations of Large Pelagic Sharks Above
558	Seamounts. In: Pitcher TJ, Morato T, Hart PJB, Clark lcolm R, Haggan N, Santos RS
559	eds. Seamounts: Ecology, Fisheries & Conservation. Blackwell Publishing Ltd, 202-206.
560	Lueck RG., Mudge TD. 1997. Topographically Induced Mixing Around a Shallow Seamount.
561	Science 276:1831–1833. DOI: 10.1126/science.276.5320.1831.

- 562 McClain C. 2007. Seamounts: identity crisis or split personality? Journal of Biogeography
- 563 34:2001–2008. DOI: 10.1111/j.1365-2699.2007.01783.x.
- 564 McClain CR., Lundsten L. 2015. Assemblage structure is related to slope and depth on a deep
- 565 offshore Pacific seamount chain. *Marine Ecology* 36:210–220. DOI:
- 566 10.1111/maec.12136.
- 567 Morato T., Varkey D., Damaso C., Machete M., Santos M., Prieto R., Santos R., Pitcher T. 2008.
- 568 Evidence of a seamount effect on aggregating visitors. *Marine Ecology-Progress Series*569 357:23–32. DOI: 10.3354/meps07269.
- 570 Morato T., Hoyle SD., Allain V., Nicol SJ. 2010a. Seamounts are hotspots of pelagic
- biodiversity in the open ocean. *Proceedings of the National Academy of Sciences*107:9707–9711. DOI: 10.1073/pnas.0910290107.
- 573 Morato T., Hoyle SD., Allain V., Nicol SJ. 2010b. Tuna Longline Fishing around West and
- 574 Central Pacific Seamounts. *PLOS ONE* 5:e14453. DOI: 10.1371/journal.pone.0014453.
- 575 Morato T., Miller PI., Dunn DC., Nicol SJ., Bowcott J., Halpin PN. 2015. A perspective on the
- 576 importance of oceanic fronts in promoting aggregation of visitors to seamounts. *Fish and*
- 577 *Fisheries*:n/a-n/a. DOI: 10.1111/faf.12126.
- 578 Morato T., Clark MR. 2007. Seamount Fishes: Ecology and Life Histories. In: Pitcher TJ,
- 579 Morato T, Hart PJB, Clark lcolm R, Haggan N, Santos RS eds. Seamounts: Ecology,
- 580 *Fisheries & Conservation*. Blackwell Publishing Ltd, 170–188.
- 581 Rogers AD. 1994. The biology of seamounts. *Advances in Marine Biology* 30:305–305.
- 582 Rutherford S., D'Hondt S., Prell W. 1999. Environmental controls on the geographic distribution
- 583 of zooplankton diversity. *Nature* 400:749–753.

NOT PEER-REVIEWED

584	Sala E., Aburto-Oropeza O., Paredes G., Thompson G. 2003. Spawning aggregations and
585	reproductive behavior of reef fishes in the Gulf of California. Bulletin of Marine Science
586	72:103–121.
587	Schaefer K., Fuller D., Block B. 2007. Movements, behavior, and habitat utilization of yellowfin
588	tuna (Thunnus albacares) in the northeastern Pacific Ocean, ascertained through archival
589	tag data. Marine Biology 152:503-525. DOI: 10.1007/s00227-007-0689-x.
590	Staudigel H., Koppers A., Lavelle JW., Pitcher T., Shank T. 2010. Defining the Word
591	"Seamount." Oceanography 23:20–21. DOI: 10.5670/oceanog.2010.85.
592	Trasvina-Castro A., de Velasco GG., Valle-Levinson A., Gonzalez-Armas R., Muhlia A., Cosio
593	MA. 2003. Hydrographic observations of the flow in the vicinity of a shallow seamount
594	top in the Gulf of California. Estuarine Coastal and Shelf Science 57:149–162.
595	Whitehead H., McGill B., Worm B. 2008. Diversity of deep-water cetaceans in relation to
596	temperature: implications for ocean warming. Ecology Letters 11:1198–1207. DOI:
597	10.1111/j.1461-0248.2008.01234.x.
598	Wolanski E., Hamner WM. 1988. Topographically Controlled Fronts in the Ocean and Their
599	Biological Influence. Science 241:177–181.
600	Worm B., Sandow M., Oschlies A., Lotze H., Myers R. 2005. Global patterns of predator
601	diversity in the open oceans. Science 309:1365–1369. DOI: 10.1126/science.1113399.
602	Worm B., Lotze H., Myers R. 2003. Predator diversity hotspots in the blue ocean. Proceedings of
603	the National Academy of Sciences 100:9884–9888. DOI: 10.1073/pnas.1333941100.
604	Wright DH. 1983. Species-energy theory: an extension of species-area theory. Oikos:496-506.
605	

607 Tables.

amily or Class	Common Name	Species	Environment*
Carangidae	Green jack	Caranx caballus	Pelagic-neritic
	Jack mackerel	Trachurus symmetricus	Pelagic-oceanic
	Mackerel scad	Decapterus macarellus	Pelagic-oceanic
	Yellowtail	Seriola lalandi	Benthopelagic
	Amberjack	Seriola rivoliana	Reef-associated
	Gafftopsail pompano	Trachinotus rhodopus	Reef-associated
Chondrichthyes	Hammerhead shark	Sphyrna lewini	Pelagic-oceanic
	Silky shark	Carcharhinus falciformis	Reef-associated
	Whale shark	Rhincodon typus	Pelagic-oceanic
	Manta	Manta hamiltoni	Reef-associated
Coryphaenidae	Dorado	Coryphaena hippurus	Pelagic-neritic
stiophoridae	Sailfish	Istiophorus platypterus	Pelagic-oceanic
*	Striped marlin	Tetrapterus audax	Pelagic-oceanic
	Blue marlin	Makaira mazara	Pelagic-oceanic
Lutjanidae	Red snapper	Lutjanus peru	Reef-associated
	Yellow snapper	Lutjanus argentriventris	Reef-associated
	Mullet snapper	Lutjanus aratus	Reef-associated
	Dog snapper	Lutjanus novenfasciatus	Reef-associated
	Colorado snapper	Lutjanus colorado	Reef-associated
	Barred snapper	Hoplopagrus guntherii	Reef-associated
	Rose-spotted snapper	Lutjanus guttatus	Reef-associated
Scombridae	Yellowfin tuna	Thunnus albacares	Pelagic-oceanic
	Black skipjack	Euthynnus lineatus	Pelagic-oceanic
	Wahoo	Acanthocybium solandri	Pelagic-oceanic
Serranidae	Creolfish	Paranthias colonus	Reef-associated
	Gulf grouper	Mycteroperca jordani	Reef-associated
	Leopard grouper	Mycteroperca rosacea	Reef-associated

656	
657	
658	Table 2. The bin centers and ranges corresponding to
659	ordinal scores for underwater visual census counts.
660	Repeated censuses were averaged and then assigned
661	ordinal scores according to the following log ₂
662	classification scheme.
663	
664	
665	

665			
666	Ordinal	Bin	Bin
667	Score	center	range
668			
669			
670	0	0	0
671	1	$1(2^0)$	$0 - 2^{0.5}$
672	2	$2(2^{1})$	2 ^{0.5} - 2 ^{1.5}
673	3	$4(2^2)$	2 ^{1.5} - 2 ^{2.5}
674	4	8 (23)	2 ^{2.5} - 2 ^{3.5}
675	5	16 (24)	2 ^{3.5} - 2 ^{4.5}
676	6	$32(2^5)$	2 ^{4.5} - 2 ^{5.5}
677	7	$64(2^6)$	2 ^{5.5} - 2 ^{6.5}
678	8	128 (27)	> 2 ^{6.5}
679			
680			
681			
682			

Table 3. Ordinal values from underwater visual counts of fishes at El Bajo Espiritu seamount from 1999-2004 by month. Each value
 represents the mean number of individuals counted per number of transects. nd indicates no data.
 685
 686

687																											
688 689			199	99		20	000		20	001			20	002					2003	3				20	04		
690 691		Ma	ıy Au	g Nov	Feb	Apr	Jun	Sep	Mai	Jul	Jun	Jul	Sep	Oct	Nov	Dec	Feb	Ma	r May	/ Oct	t Nov	Jan	Арі	May	Jun	Jul	Aug
692																											
693	Caranx caballus	0	8	8	0	0	8	8	0	8	7	0	7	6	4	4	0	0	0	1	5	0	0	8	8	8	8
694	Decapterus macarellus	8	8	8	7	7	8	8	7	8	7	6	6	6	7	8	0	7	8	7	8	8	8	8	8	8	7
695	Euthynnus lineatus	8	8	8	7	2	6	0	6	7	6	4	8	0	0	0	0	4	8	0	7	0	7	8	0	8	2
696	Lutjanus argentriventris	8	8	7	1	7	7	7	7	4	4	6	7	8	5	8	4	5	0	8	7	5	8	8	8	8	7
697	Lutjanus colorado	0	0	0	0	0	1	0	0	3	0	0	0	5	0	2	0	1	0	0	7	0	0	0	7	2	5
698	Hoplopagrus guntherii	4	4	4	0	4	0	4	2	0	0	0	2	5	0	1	3	3	1	2	3	2	1	4	1	3	3
699	Lutjanus novemfasciatus	0	5	3	0	0	0	8	0	1	0	0	5	0	0	0	0	0	0	1	4	1	1	0	0	0	0
700	Lutjanus peru	8	2	0	7	8	0	0	7	6	6	7	0	0	0	0	0	0	8	0	0	0	1	8	2	3	0
701	Mycteroperca jordani	nd	nd	nd	3	2	3	0	2	0	1	1	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0
702	Mycteroperca rosacea	nd	nd	nd	nd	3	0	0	4	3	3	1	2	3	3	2	2	3	3	2	3	3	1	4	2	4	0
703	Paranthias colonus	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	7	8	8	8	8	8	8	8	0	7
704	Seriola lalandi	0	0	0	4	3	0	0	3	0	1	0	0	0	0	0	4	3	0	0	0	4	0	0	0	1	0
705	Seriola rivoliana	4	1	0	4	0	2	0	4	3	2	1	0	0	0	0	0	2	4	0	0	2	2	1	1	0	0
706	Sphyrna lewini	0	6	3	2	0	0	0	4	0	1	2	0	5	3	6	5	3	1	4	6	0	0	0	0	0	4
707																											
708	Number of replicates	2	2	2	2	2	1	1	4	2	4	2	2	2	3	2	2	2	2	1	2	2	2	1	2	2	2
709																											
710																											

Table 4. Presence or absence of species from both dive and fishing surveys observed by month. 711

Species were given a positive score (•) if they were ever observed during the month over the 5-712 713 year study period.

						Mo	onth						
		1	2	3	4	5	6	7	8	9	10	11	1
Fall													
(Caranx caballus					٠	•	•	٠	•	٠	•	•
(Coryphaena hippurus						•		٠	•	٠	•	
1	Lutjanus argentriventris	٠	٠	•	٠	٠	٠	•	٠	٠	٠	٠	
1	Lutjanus novemfasciatus	٠			٠			•	٠	•	•	•	
2	Sphyrna lewini		•	•		•	•	٠	٠		٠	٠	•
Sprin	ng												
1	Lutjanus peru		٠	•	٠	٠	•	•	٠				
1	Mycteroperca jordani		٠	٠	٠		•	•					
S	Seriola lalandi	•	٠	٠	٠		•	•					
S	Seriola rivoliana	•	٠	•	٠	٠	•	٠	٠				
Year	r-round												
Ŀ	Acanthocybium solandri					٠	•		٠		•	•	
1	Decapterus macarellus	•	٠	•	٠	٠	•	•	٠	•	٠	•	
l	Euthynnus lineatus		٠	•	٠	٠	٠	٠	٠	•		٠	
l	Hoplopagrus guntherii	•	٠	•	٠	٠	٠	٠	٠	•	•	٠	
1	Lutjanus colorado			•			•	•	٠		٠	•	
1	Mycteroperca rosacea	•	٠	•	٠	٠	٠	٠		•	•	٠	
I	Paranthias colonus	•	٠	•	٠	٠	٠	•	٠	•	٠	•	
7	Thunnus albacares		٠			٠	•		•	٠			

738 Figures.

739

Fig. 1 Map of the Southern Gulf of California and Eastern Pacific Ocean overlain with NOAA
AVHRR sea surface temperature (SST). Images from (A) February 4, 2004, and (B) August 2,
2003 recorded respectively during seasonal high and low peaks of the annual temperature cycle.
(C) Sea surface temperature (gray line) and subsurface temperature (black line), measured at a
depth of 30 m (T30), at El Bajo Espiritu Santo seamount (EBES; see filled circle in panel A).





747

748

Fig. 2 Water column profiles of temperature immediately adjacent to El Bajo Espiritu Santo
seamount. Stratification above 30 m (dashed line) ranged from strong in June to very weak in
November.

752



754

NOT PEER-REVIEWED

Peer Preprints

Fig. 3 Relative abundance of representative species. Illustrative examples from the spring (A) *Seriola lalandi* and fall (B) *Lutjanus novemfasciatus* assemblages of fishes relative to mean
monthly SST (gray line) and T30 (dark line) at El Bajo Espiritu Santo seamount from 19992005. Note that broken line portions in the T30 series represent estimated values for missing
data.

760



763

761

Fig. 4 Ordination analysis of seamount fish species assemblages. Negative log likelihood parameter estimates of the two regressors, sea surface temperature (SST) and temperature at 30 m (T30), from logistic regression plotted on the plane $\gamma = \rho + \beta + SST + \beta T30$ revealed a spring (upper right) and fall (lower left) assemblage. Error bars represent standard error. Dark circles resulted from ordinal regression, and open circle resulted from nominal regression.



769

Fig. 5 Species abundance curves over time. These qualitatively illustrate the occurrence of 772

773 seasonal peaks in relative abundance of various fish species at El Bajo Espiritu Santo (EBES)

774 seamount. These species comprised the (A) fall, (B) spring and (C) year-round assemblages

775 respectively grouped based on logistic regression analysis output.

776



NOT PEER-REVIEWED

Peer Preprints

- 779 Fig. 6 Linear relationship between number of species and vertical thermal gradient at El Bajo
- 780 Espiritu Santo seamount. The number of observed species increased in months with greater
- 781 stratification (n = 12 months, $r^2 = 0.587$, p = 0.004).
- 782

783

