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Distribution of fish larvae on the Vitória-Trindade Chain, southwestern Atlantic

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Abstract: This work presents a checklist of ichthyoplankton collected along the Vitória-Trindade chain with oblique bongo hauls to a depth of 20 m in the summer and in the winter. Larvae were classified according the adult habitat as reef, epipelagic or mesopelagic. The variables season, depth, sampling time, environment type and distance from the continental shelf were used to test the correlation with the larval density of each larval category. In the summer, 3,897 larvae were captured (identified at the family, genera or species level, *n* = 44, 33 and 82, respectively) and 1,026 larvae were captured in the winter (19, 17 and 25, respectively). Only the variables season and environment type significantly affected density, with their influence varying among larval categories.

Key words: plankton, seamounts, Brazil

INTRODUCTION

The Vitória-Trindade chain (VTC) extends for about 1,160 km east off the coast of Espírito Santo state, Brazil. It consists of about 30 seamounts (Motoki et al. 2012), several relatively shallow, reaching depths of less than 50 m. The seamounts Vitória (1,184 km² of plateau above the 120 m isobath), Montague (124 km²), Jaseur (89 km²), Davis (1,002 km²), Dogaressa (80.5 km²), and Columbia (36.5 km²), as well as the Trindade Island (85 km²) and Martin Vaz Archipelago (24 km²; Figure 1), are the largest and main features of the VTC. These seamounts and islands are separated by bathyal and abyssal depths and distances between 50 and 225 km (Motoki et al. 2012), the latter being the distance between Trindade and Columbia. The VTC and the Abrolhos Shelf are considered, together, a marine area ecologically and biologically significant for conservation (UNEP 2012).

The insular complex Trindade-Martin Vaz (the two islands are separated by less than 50 km) contains 154 fish species (Simon et al. 2013). While 21.6% of coastal fishes of Trindade have a circumglobal distribution, 27.5% are only found in the tropical Atlantic Ocean, 43.1% are restricted to the western Atlantic and 7.8% are endemic to the island complex (Simon et al. 2013). The similarity observed between the ichthyofauna of Trindade and that of the South American coast suggests that reef fishes use seamounts and island of the VTC as stepping-stones (Gasparini and Floeter 2011). Hypothetically, fishes and other organisms would have colonized the summit of seamounts in succession from the initial area of exportation of species (*a priori,* the continental shelf) to the final receiving area (in this case, Trindade and Martin Vaz). Gene flow between

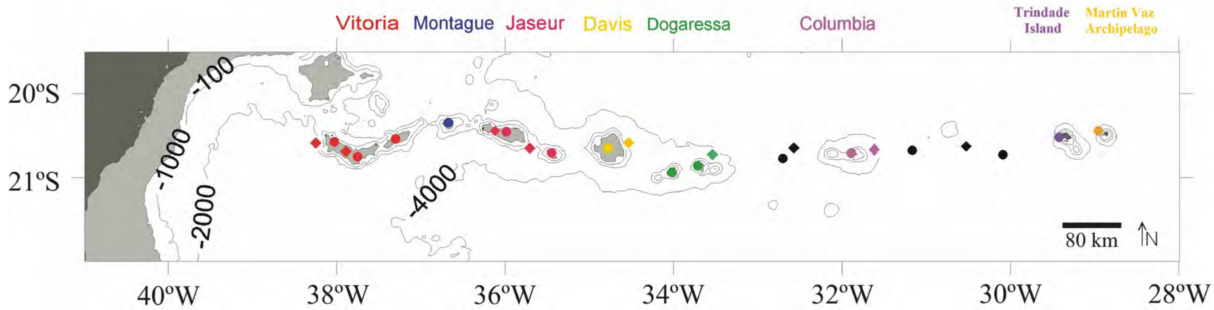

Figure 1. Collection points and locations sampled along the Vitória-Trindade Chain. The circles represent the collections made in summer (December 2011) and the diamonds those made in winter (July 2013). Locations are color-coded. Note that the four collection points near Trindade Island are represented by a single symbol, as are the four points near Martin Vaz Archipelago.

subpopulations could be maintained according to the same scheme (Kimura 1953). Transport over long distances of open sea is made possible by the dispersal ability characteristic of the planktonic phase. For eggs and larvae insufficiently developed, the displacement is entirely passive and promoted by the movement of water masses. Due to their swimming capacity, larvae in the most advanced stages of development are potentially able to position themselves in a particular water mass in which they can be transported or retained (Leis 1991; Huebert et al. 2010). For reef fishes, retention processes are especially important to stay close to the reef (Leis 1991). Epipelagic fish spawn off the coast or near islands, where the larvae can remain to feed (Mather et al. 1995; Alemany et al. 2010; D'Alessandro et al. 2011). Mesopelagic larvae, on the other hand, hatch at great depths and perform vertical migration according to their stage of ontogenic development (Richards 2006).

The study of oceanic ichthyoplankton in the Southeast and South of Brazil has intensified since the 1960s (Katsuragawa et al. 2006) with important works from the Abrolhos Shelf (Nonaka et al. 2000) to Rio Grande do Sul state (Matsuura and Kitahara 1995; Franco and Muelbert 2003), including the Cabo Frio upwelling region (Freitas and Muelbert 2004; Gasalla et al. 2007). Ichthyoplankton surveys on the VTC were conducted before by the REVIZEE program between 1998 and 2000 (Bonecker et al. 2006; Bonecker and Castro 2006; Castro 2006), but this faunal component remains poorly known despite its scientific and biological importance. This work presents a checklist for ichthyoplankton from the VTC and tests the hypotheses that larval density (1) varies between seasons, likely in response to reproductive periodicity; (2) varies with depth according to the habitat used by adults; (3) is higher during the nocturnal period, when occurs the vertical migration; (4) differs among seamount, island and deep ocean because of their distinct oceanographic, chemical and biological aspects; and (5) decreases with distance from the continental shelf following the idea that larval density of topographically associated species often decreases with increasing distance of seamounts from larger land masses (Boehlert and Mundy 1993).

MATERIAL AND METHODS

The ichthyoplankton was collected in summer (December 2011) by NOc Antares and in winter (July 2013) by NHo Cruzeiro do Sul with a bongo net (60 cm aperture, 3 m long and 570 μm mesh in the cod-end) equipped with a mechanical flowmeter (General Oceanics). A total of 10 locations were sampled: Vitória, Montague, Jaseur, Davis, Dogaressa and Columbia seamounts, Trindade and Martin Vaz islands, and stretches of open ocean between Dogaressa and Columbia and between Columbia and Trindade. Twenty-one stations were sampled in the summer, 13 along the chain, four near Trindade and four near Martin Vaz (Figure 1). Two hauls were made at each station, resulting in 84 samples. In each haul, one sample was fixed in 10% formalin and the other in alcohol 93%. Nine stations were sampled in the winter (Figure 1) with one oblique haul at each station, resulting in 18 samples that were fixed in alcohol 93%. Hauls in both seasons were oblique to a depth of 20 m, lasted between 10 and 20 minutes and were done at a speed of approximately 2 knots. Depth at station was recorded from the ship's sonar.

Larvae were identified to the lowest taxonomic level as per Fahay (1983), Bonecker and Castro (2006), Richards (2006) and Victor (2012). They were further classified according to the type of habitat occupied by adults (reef, epipelagic and mesopelagic) following Richards (2006) and Froese and Pauly (2012). The reef larvae are those taxa that in the adult phase are associated with the bottom, either reef or marginal areas (e.g., rhodolith beds or sand); the epipelagic larvae contains those pelagic taxa that live in the photic zone of the water column; and the mesopelagic larvae comprise those pelagic taxa that generally occupy the aphotic zone during the day and feed in the upper layers of the water column at night.

The density (larvae 100 m^{-3}) at each station was calculated as the ratio between number of individuals and total volume filtered. The density of reef, mesopelagic and epipelagic taxa was analyzed concomitantly using type III multifactorial MANOVA. Note that conditions to apply such analysis are not optimal due, among others, to the unbalanced design and the low number of values. Fixed factors were seasons (summer and winter; n = 21 and 9, respectively), depth at the place of sampling (categorized in three classes: 0–100 m, 100–1000 m and 1000 m or more; n = 12, 5 and 13), sampling time (day and night; n = 15 and 15), environment type (three classes: seamount, island and deep ocean between seamounts and island; n = 17, 8 and 5) and position according distance of the continental shelf (in the following order: Vitória, Montague, Jaseur, Davis, Dogaressa, Dogaressa-Columbia, Columbia, Columbia-Trindade, Trindade Island and Martin Vaz Archipelago; n= 5, 1, 4, 2, 3, 2, 2, 3, 4 and 4). Density data were log-transformed [ln(x+1)] prior to analysis, and homogeneity of variance checked by Levene test. A stepwise removal of least-significant variables (α = 0.05) was performed to optimize the available number of degrees of freedom (df = 29) to the high number of df used (only main effects were included; df = 15). MANOVA results indicated if the larval categories relative to the habitat of adults responded differently in respect to the independent variables inserted in the model. The best MANOVA model was further explored with ANOVAs for each dependent variable (density of reef, epipelagic and mesopelagic larvae) using MANOVA-selected explanatory variables. *A posteriori* Tukey HSD tests were applied in order to detect differences between categories. All MANOVA and ANOVA tests were run on IBM SPSS Statistic Version 20.0.

RESULTS

Almost four thousand (3,897) larvae were collected in summer and that were distributed in 159 taxa identified at the family (n = 44), genus (n = 33) or species level (n = 82) (Table 1). Due to their poor condition or because they were in the early stages of ontogenetic development, 13.3% of larvae were not identified but classified into 38 morphogroups (UNID, i.e., unidentified). In the winter, 1,026 larvae belonging to 61 taxa were collected and identified at the family level (19), genus (17) or species (25) level. Only one winter taxon was classified as UNID.

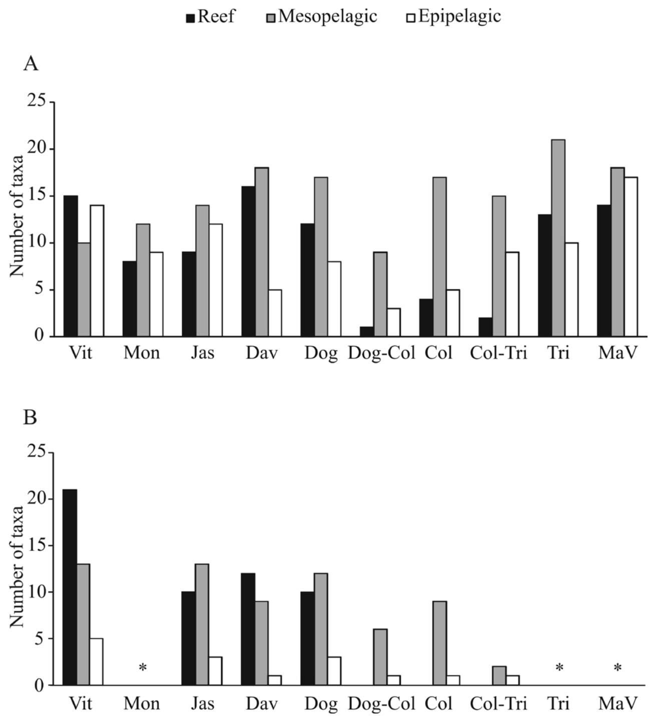

Figure 2. Density (individuals·100 m^{-3}) of reef, mesopelagic and epipelagic taxa collected along the Vitória-Trindade Chain in summer (A) and in winter (B) according to location (see Table 1 for abbreviations). *[1] Vertical axis in A was truncated; observed valors are: Vit: 177 ind·100m^{-3}; Dav: 106 ind·100m^{-3}; Col: 118 ind·100m^{-3}. *[2] Not sampled.

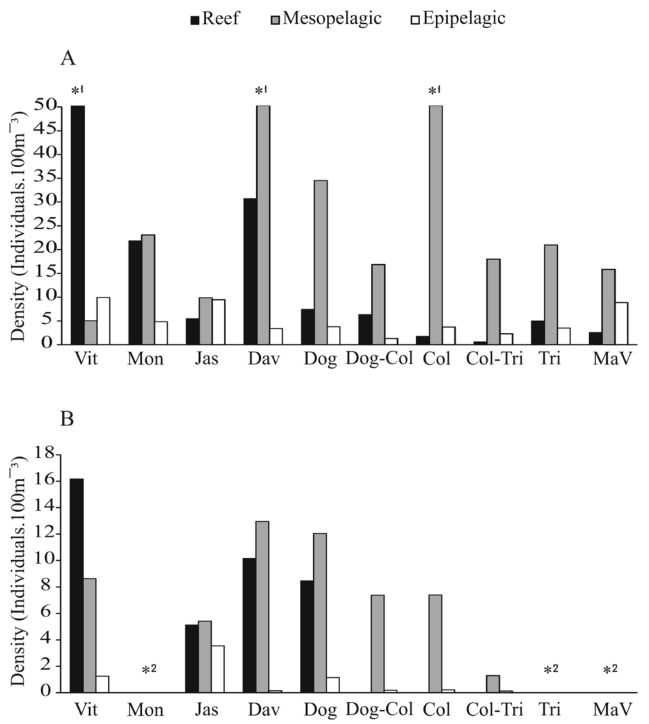

Figure 3. Number of reef, mesopelagic and epipelagic taxa collected along the Vitória-Trindade Chain in summer (A) and in winter (B) according to location (see Table 1 for abbreviations). * Not sampled.

Mesopelagic larvae were the most abundant at all locations, except for Vitória (Figure 2). Myctophidae and Gonostomatidae represented, respectively, 27 and 13% of total larvae in summer and Myctophidae remained the most abundant family in winter (34%) (Table 1). The family Scombridae (7% of total larvae) and the species *Ranzania laevis* (Pennant, 1776) (1%) were the most abundant epipelagic taxa in summer while the species *Gempylus serpens* Cuvier, 1829 was the most common (6%) in winter. Holocentridae (23% of total), Labridae (4%) and Serranidae (2%) were the most abundant reef taxa in summer while in winter Serranidae (18%) and Pomacanthidae (5%) dominated. About 99% of Holocentridae were collected on Vitória seamount in two summer stations. Mesopelagic larvae had the highest number of taxa at all locations (Figure 3) except at Vitória (in the two seasons) and at Davis (in winter) where reef larvae were the most diverse.

The stepwise MANOVA testing the density of reef, epipelagic and mesopelagic taxa was significant (Pillai's Trace test; P < 0.001) when including season (Wilks' Lambda: P < 0.001) and environment type (P = 0.01). (The categorical variables depth at the place of sampling—amply redundant with environment type—sampling time and distance from the continental shelf were not significant and removed from the model.) Thus, the three larval categories based on adult habitat behave differently in respect to the explanatory variables. Reef taxa were significantly more abundant over seamounts than in open ocean locations (ANOVA, Tukey post-hoc test; P = 0.021) while epipelagic larvae were significantly more abundant near islands (P = 0.03) and over seamounts (P = 0.043) than far from such geological structures (Table 2). The density of epipelagic taxa was higher in the summer (P < 0.001; Table 2).

DISCUSSION

Mesopelagic larvae numerically dominate the VTC ichthyoplankton community with no discernible variation in space or time. On the other hand, reef and epipelagic larvae appear dependent upon the presence of relief (seamounts or islands) and larval density of epipelagic taxa peaked in summer, likely in response to reproduction. The fish larvae community composition observed over the Vitória-Trindade chain is similar to those described for other regions of the tropical and subtropical southwestern Atlantic (Katsuragawa and Matsuura 1990; Ekau et al. 1999; Nonaka et al. 2000; Bonecker et

Table 1. Ichthyoplanktonic taxa of the Vitória-Trindade Chain. Percentage of individuals in relation to total captured, P(%) in summer (Su) and winter (Wi), occurrence in the seamounts and islands of VTC (● in summer and ♦ in winter) and adult habitat (AH). Families are presented in phylogenetic order (Nelson 2006) and species in alphabetical order. The family Labridae includes Scarinae (Westneat and Alfaro 2005). Occurrence: **Vit**: Vitória; **Mon**: Montague; **Jas**: Jaseur; **Dav**: Davis; **Dog**: Dogaressa; **Dog-Col**: between Dogaressa and Columbia seamounts; **Col**: Columbia; **Col-Tri**: between Columbia seamount and Trindade Island; **Tri**: Trindade Island; **MaV**: Martin Vaz Archipelago. **UNID**: not identified.

Taxa	P(%) Su	P(%) Wi	Vit	Mon	Jas	Dav	Dog	Dog-Col	Col	Col-Tri	Tri	MaV	AH
Moringuidae	0.03												
Moringua edwardsi (Jordan & Bollman, 1889)	0.03						●						Reef
Chlopsidae	0.03												
Kaupichthys hyoproroides (Strömman, 1896)	0.03						●						Reef
Muraenidae	0.05												
Gymnothorax moringa (Cuvier, 1829)	0.03					●							Reef
Unidentified	0.03										●		Reef
Nemichthyidae	0.03	0.09											
Avocettina sp.	0.03					●							Mesopelagic
Unidentified		0.09						♦					Mesopelagic
Gonostomatidae	13.37	2.04											
Cyclothone acclinidens Garman, 1899	1.9	0.29	♦	●	●	●	●	●♦	●	●	●	●	Mesopelagic
Cyclothone braueri Jespersen & Tåning, 1926	0.03						●						Mesopelagic
Cyclothone pseudopallida Mukhacheva, 1964	0.05								●				Mesopelagic
Cyclothone sp.	11.31	1.46	●♦	●	●♦	●	●♦	●♦	●♦	●♦	●	●	Mesopelagic
Diplophos taenia Günther, 1873	0.05	0.29			♦				●♦	●			Mesopelagic
Gonostoma atlanticum Norman, 1930	0.03						●						Mesopelagic
Sternoptychidae	1.77	7.89											
Maurolicus stehmanni Parin & Kobyliansky, 1993	1.77	7.89	♦		♦	●♦		●♦	●♦	●	●	●	Mesopelagic
Phosichthydae	3.90	4.77											
Vinciguerria nimbaria (Jordan & Williams, 1895)	3.85	4.77	♦	●	●♦	●♦	●♦	●♦	●	●	●	●	Mesopelagic
Vinciguerria poweriae (Cocco, 1838)	0.05			●								●	Mesopelagic
Stomiidae	0.13	0.29											
Bathophilus sp.	0.03										●		Mesopelagic
Melanostomias sp.	0.05										●	●	Mesopelagic
Unidentified	0.08	0.29	♦			♦	●				●	●	Mesopelagic
Synodonthidae	0.03	0.19											
Synodus synodus (Linnaeus, 1758)	0.03						●						Reef
Synodus sp.		0.19	♦										Reef
Evermannellidae	0.03	0.38											
Evermannella melanoderma Parr, 1928	0.05	0.09		●			♦				●		Mesopelagic
Unidentified		0.29	♦		♦								Mesopelagic
Paralepididae	0.28	0.87											
Lestidium sp.	0.03	0.49			●	♦	♦						Mesopelagic
Lestrolepis intermedia (Poey, 1868)	0.03				●								Mesopelagic
Macroparalepis brevis Ege, 1933	0.08	0.19					♦			●	●	●	Mesopelagic
Stemonosudis intermedia (Ege, 1933)	0.05									●			Mesopelagic
Unidentified	0.13	0.19	●	●	♦	●				●		●	Mesopelagic
Gigantactinidae	0.03												
Unidentified	0.03											●	Mesopelagic
Myctophidae	30.90	33.72											
Benthosema suborbitale (Gilbert, 1913)	0.05								●				Mesopelagic
Bolinichthys sp.	0.18	1.55				●♦	●♦	●	♦	●			Mesopelagic
Centrobranchus nigroocellatus (Günther, 1873)	0.03						●						Mesopelagic
Ceratoscopelus warmingii (Lütken, 1892)	0.98	4.67	♦		●♦	●♦	●♦	●	●♦	●	●		Mesopelagic
Ceratoscopelus sp.	0.05						●						Mesopelagic
Diaphus metopoclampus (Cocco, 1829)	0.13				●	●						●	Mesopelagic
Diaphus mollis Tåning de, 1928	17.38	14.91	●♦	●	●♦	●♦	●♦	●♦	●♦	●♦	●	●	Mesopelagic

Continued

Table 1. *Continued.*

Taxa	P(%) Su	P(%) Wi	Vit	Mon	Jas	Dav	Dog	Dog-Col	Col	Col-Tri	Tri	MaV	AH
Diaphus sp. (as in Richards 2006)	1.64	3.08	●♦	●	●♦	●♦	●♦	●	●♦	●	●	●	Mesopelagic
Hygophum macrochir (Günther, 1864)	0.03											●	Mesopelagic
Hygophum taaningi Becker, 1965	0.03										●		Mesopelagic
Hygophum sp.	0.18	0.19							●♦				Mesopelagic
Lampadena sp.	0.56	0.39	♦	●	●	●			●			●	Mesopelagic
Lampanyctus nobilis Tåning de, 1928	0.05				●								Mesopelagic
Lepidophanes gaussi (Brauer, 1906)	2.31	3.12	●♦		●♦	●	●♦	●	●♦	●	●	●	Mesopelagic
Lepidophanes guentheri (Goode & Bean, 1896)	1.39	4.97	●♦	●	●♦	●♦	●♦		●		●	●	Mesopelagic
Lepidophanes sp.	0.05						●						Mesopelagic
Lobianchia dofleini (Zugmayer, 1911)	0.03						●						Mesopelagic
Myctophum obtusirostre Tåning, 1928	0.03				●								Mesopelagic
Nannobrachium atrum (Tåning, 1928)	0.05					●							Mesopelagic
Nannobranchium sp.	0.03										●		Mesopelagic
Notoscopelus caudispinosus (Johnson, 1863)		0.09			♦								Mesopelagic
Myctophidae 1	5.11		●	●	●	●	●	●	●	●	●	●	Mesopelagic
Myctophidae 2	0.05		●								●		Mesopelagic
Myctophidae 3	0.08			●					●		●		Mesopelagic
Myctophidae 4	0.05					●						●	Mesopelagic
Myctophidae 5	0.08					●					●		Mesopelagic
Myctophidae 6	0.03								●				Mesopelagic
Myctophidae 7	0.05									●			Mesopelagic
Myctophidae 8	0.03									●			Mesopelagic
Myctophidae 9	0.28									●	●		Mesopelagic
Radiicephalidae	0.03												
Unidentified	0.03											●	Mesopelagic
Trachipteridae	0.05												
Trachipterus trachypterus (Gmelin, 1789)	0.03						●						Mesopelagic
Zu cristatus (Bonelli, 1819)	0.03											●	Mesopelagic
Bregmacerotidae		0.09											
Bregmaceros atlanticus Goode & Bean, 1886		0.09				♦							Mesopelagic
Ophidiidae	0.13	0.09											
Spectrunculus grandis (Günther, 1877)	0.03								●				Mesopelagic
Unidentified	0.11	0.09	●♦			●				●			Mesopelagic
Ceratiidae	0.03												
Cryptopsaras couesii Gill, 1883	0.03	0.09									●		Mesopelagic
Unidentified		0.09			♦								Mesopelagic
Belonidae	0.05												
Unidentified	0.05										●	●	Epipelagic
Exocoetidae	0.56												
Cheilopogon exsiliens (Linnaeus, 1771)	0.10				●		●	●		●			Epipelagic
Cheilopogon furcatus (Mitchill, 1815)	0.03											●	Epipelagic
Exocoetus volitans Linnaeus, 1758	0.15				●						●	●	Epipelagic
Exocoetus sp.	0.08				●			●				●	Epipelagic
Unidentified	0.20									●		●	Epipelagic
Hemiramphidae	0.08												
Unidentified	0.08		●	●								●	Epipelagic
Trachichthyidae	0.03												
Unidentified	0.03									●			Mesopelagic
Holocentridae	23.25	0.48											
Unidentified	23.25	0.48	●♦		♦	●	●	●				●	Reef
Syngnathidae	0.05	0.09											
Amphelikturus dendriticus (Barbour, 1905)	0.03					●							Reef
Micrognathus crinitus (Jenyns, 1842)	0.03					●							Reef
Unidentified		0.09	♦										Reef
Aulostomidae	0.03												
Aulostomus strigosus Wheeler, 1955	0.03											●	Reef

Continued

Table 1. *Continued.*

Taxa	P(%) Su	P(%) Wi	Vit	Mon	Jas	Dav	Dog	Dog-Col	Col	Col-Tri	Tri	MaV	AH
Fistulariidae	0.03												
Fistularia petimba Lacepède, 1803	0.03			●									Reef
Dactylopteridae	0.21												
Dactylopterus volitans (Linnaeus, 1758)	0.21		●		●								Reef
Scorpaenidae	0.44	0.29											
Unidentified	0.44	0.29	●♦	●	●	●	●					●	Reef
Serranidae	1.54	18.21											
Anthias sp.	0.05	0.09	●				●♦						Reef
Epinephelus sp.	0.03		●										Reef
Liopropoma carmabi (Randall, 1963)	0.15			●			●						Reef
Pseudogramma gregoryi (Breder, 1927)	0.13			●			●					●	Reef
Serranus sp.	0.44	18.12	●♦		♦	●♦	●♦				●	●	Reef
Serranidae 1	0.15					●							Reef
Serranidae 2	0.46					●							Reef
Unidentified	0.13		●		●				●		●		Reef
Opistognathidae	0.08	1.17											
Opistognathus aurifrons (Jordan & Thompson, 1905)	0.08										●		Reef
Unidentified		1.17	♦			♦	♦						Reef
Apogonidae	0.26	3.21	♦		♦	♦	♦						
Apogon sp.	0.15	2.83			♦	♦ ●	♦					●	Reef
Phaeoptyx sp.	0.03	0.38	♦				●						Reef
Unidentified	0.08					●					●		Reef
Epigonidae	0.03												
Unidentified	0.03									●			Reef
Coryphaenidae	0.10	0.48											
Coryphaena equiselis Linnaeus, 1758	0.10	0.39	♦●		♦					●		●	Epipelagic
Coryphaena hippurus Linnaeus, 1758		0.09			♦								Epipelagic
Echeneidae	0.13												
Echeneis naucrates Linnaeus, 1758	0.08											●	Epipelagic
Unidentified	0.05						●	●					Epipelagic
Carangidae	0.98	2.43											
Caranx sp.	0.31		●										Reef
Decapterus macarellus (Cuvier, 1833)	0.13	2.04	♦ ●		♦	♦	♦						Reef
Oligoplites saurus (Bloch & Schneider, 1801)	0.03				●								Reef
Pseudocaranx dentex (Bloch & Schneider, 1801)	0.05		●										Reef
Selar crumenophthalmus (Bloch, 1793)	0.10	0.09	●				♦						Reef
Seriola zonata (Mitchill, 1815)	0.05		●										Reef
Unidentified	0.31	0.29	♦ ●			●						●	Reef
Bramidae	0.03												
Unidentified	0.03		●										Epipelagic
Lutjanidae	0.23												
Lutjanus sp.	0.18										●		Reef
Unidentified	0.05											●	Reef
Mullidae	0.26	3.70											
Unidentified	0.26	3.70	●♦			♦	♦						Reef
Chaetodontidae		0.09											
Unidentified		0.09	♦										Reef
Pomacanthidae	0.15	5.06											
Centropyge sp.	0.03										●		Reef
Holacanthus tricolor (Bloch, 1795)	0.10	2.53	♦		♦		●		●			●	Reef
Unidentified	0.03	2.53	●♦		♦	♦							Reef
Cirrhitidae	0.08												
Amblycirrhitus pinos (Mowbray, 1927)	0.08			●	●								Reef
Pomacentridae	0.26	0.58											
Chromis sp.	0.03	0.29	♦						●				Reef
Microspathodon chrysurus (Cuvier, 1830)	0.08										●	●	Reef
Stegastes sp.	0.10		●			●				●		●	Reef
Unidentified	0.05	0.29	♦			●♦							Reef

Continued

Table 1. *Continued.*

Taxa	P(%) Su	P(%) Wi	Vit	Mon	Jas	Dav	Dog	Dog-Col	Col	Col-Tri	Tri	MaV	AH
Labridae	3.95	3.39											
Cryptotomus roseus Cope, 1871	1.57	2.04	♦	●	●♦	●♦	●♦						Reef
Doratonotus megalepis Günther, 1862	0.41	0.09	●♦			●							Reef
Halichoeres sp.	0.03										●		Reef
Scarus sp.	0.05	0.29		●	♦		♦					●	Reef
Sparisoma sp.	1.18	0.39	♦	●	●		♦						Reef
Xyrichtys sp.	0.03										●		Reef
Unidentified	0.70	0.58	♦		●	●♦					●	●	Reef
Chiasmodontidae	0.05												
Kali macrura (Parr, 1933).	0.03											●	Mesopelagic
Pseudoscopelus sp.	0.03								●				Mesopelagic
Gobiesocidae	0.13												
Unidentified	0.13										●		Reef
Callionymidae		0.09											
Callionymus bairdi Jordan, 1888		0.09				♦							Reef
Gobiidae	1.08												
Coryphopterus sp.	0.18					●					●	●	Reef
Elacatinus sp.	0.08					●							Reef
Gnatholepis thompsoni Jordan, 1904	0.03						●						Reef
Lythrypnus sp.	0.18										●		Reef
Unidentified	0.62						●				●	●	Reef
Ptereleotridae	0.18	1.36											
Ptereleotris randalii Gasparini, Rocha & Floeter, 2001	0.18	1.36	♦			●♦	♦						Reef
Sphyraenidae	0.33	0.68											
Sphyraena barracuda (Edwards, 1771)	0.08	0.09	●				●♦				●		Epipelagic
Sphyraena guachancho Cuvier, 1829	0.05				●								Epipelagic
Sphyraena picudilla Poey, 1860	0.10	0.48	♦				●					●	Epipelagic
Sphyraena sp.	0.10	0.09	●♦	●	●						●		Epipelagic
Gempylidae	0.51	5.94											
Gempylus serpens Cuvier, 1829	0.51	5.94	●♦	●	●♦		♦		●♦	●♦	●	●	Epipelagic
Scombridae	6.85	0.68											
Acanthocybium solandri (Cuvier, 1832)	0.05			●								●	Epipelagic
Euthynnus alletteratus (Rafinesque, 1810)	0.08		●									●	Epipelagic
Katsuwonus pelamis (Linnaeus, 1758)	0.90	0.29	●♦	●	●	●♦	●	♦		●	●		Epipelagic
Scomber colias Gmelin, 1789	0.03					●							Epipelagic
Scomberomorus cavalla (Cuvier, 1829)	0.05		●										Epipelagic
Thunnus alalunga (Bonnaterre, 1788)	3.08		●	●	●	●	●		●	●	●	●	Epipelagic
Thunnus albacares (Bonnaterre, 1788)	1.51		●	●	●	●	●		●	●	●	●	Epipelagic
Thunnus obesus (Lowe, 1839)	0.18		●	●	●							●	Epipelagic
Thunnus sp.	0.13	0.09					♦				●	●	Epipelagic
Unidentified	0.85	0.29	●♦		●		●	●		●		●	Epipelagic
Istiophoridae	0.05												
Makaira nigricans Lacepède, 1802	0.03		●										Epipelagic
Unidentified	0.03				●								Epipelagic
Nomeidae	0.44												
Cubiceps pauciradiatus Günther, 1872	0.23			●									Mesopelagic
Cubiceps sp.	0.10					●							Mesopelagic
Psenes cyanophrys Valenciennes, 1833	0.10			●		●							Mesopelagic
Caproidae	0.03												
Unidentified	0.03						●						Reef
Bothidae	0.05												
Bothus lunatus (Linnaeus, 1758)	0.03										●		Reef
Bothus ocellatus (Agassiz, 1831)	0.03											●	Reef
Balistidae	0.41												
Balistes capriscus Gmelin, 1789	0.03				●								Reef
Canthidermis sufflamen (Mitchill, 1815)	0.03				●								Reef

Continued

Table 1. *Continued.*

Taxa	P(%) Su	P(%) Wi	Vit	Mon	Jas	Dav	Dog	Dog-Col	Col	Col-Tri	Tri	MaV	AH
Xanthichthys ringens (Linnaeus, 1758)	0.30		•		•	•							Reef
Unidentified	0.10					•						•	Reef
Monacanthidae	0.10	0.09											
Monacanthus ciliatus (Mitchill, 1818)	0.08		•			•							Reef
Unidentified	0.03	0.09			♦	•							Reef
Ostraciidae	1.21												
Unidentified	1.21		•	•	•	•	•	•				•	Reef
Tetraodontidae	0.18	0.09											
Sphoeroides sp.		0.09			♦								
Unidentified	0.18			•			•			•	•	•	Reef
Diodontidae	0.15	0.09											
Unidentified	0.15	0.09	♦ •						•	•		•	Reef
Molidae	1.49												
Ranzania laevis (Pennant, 1776)	1.49		•	•	•	•	•		•	•	•	•	Epipelagic
Unidentified	3.13												
UNID 1	0.03		•										
UNID 2	0.03		•										
UNID 3	0.03		•										
UNID 4	0.03		•										
UNID 5	0.13		•								•		
UNID 6	0.03		•										
UNID 7	0.03		•										
UNID 8	0.03		•										
UNID 9	0.08			•	•								
UNID 10	0.03				•								
UNID 11	0.05					•							
UNID 12	0.03					•							
UNID 13	0.08					•							
UNID 14	0.05					•							
UNID 15	0.03						•						
UNID 16	0.03						•						
UNID 17	0.03							•					
UNID 18	0.03								•				
UNID 19	0.64								•	•	•	•	
UNID 20	0.13									•	•		
UNID 21	0.05									•			
UNID 22	0.03										•		
UNID 23	0.03										•		
UNID 24	0.28										•	•	
UNID 25	0.10										•		
UNID 26	0.41										•		
UNID 27	0.05										•		
UNID 28	0.03										•		
UNID 29	0.26										•		
UNID 30	0.18												
UNID 31	0.05											•	
UNID 32	0.03											•	
UNID 33	0.03											•	
UNID 34	0.03											•	
UNID 35	0.03											•	
UNID 36	0.03											•	
UNID 37	0.03											•	
UNID 38	0.03											•	
UNID 39		1.07	♦										

Table 2. Summary of ANOVAs results for ichthyoplankton density along the VTC according to season (summer and winter) and type of environment (seamount, island or open ocean). Ichthyoplankton is categorized according to the habitat used by adults. Superscript letters indicate homogeneous groups (Tukey test) from higher (a) to lower (b) mean. The variables depth, sampling time and position according to distance of the continental shelf were not be included because they were not significant in the MANOVA.

	Adult Habitat					
	Reef		Mesopelagic		Epipelagic	
Source	**F-value**	**P-value**	**F-value**	**P-value**	**F-value**	**P-value**
Model	4.471	0.012	1.353	0.279	12.433	<0.001
Season	3.719	NS	2.694	NS	24.137	< 0.001
	_		_		Summer[a] Winter[b]	
Environment type	5.907	0.008	0.126	NS	3.498	0.045
	Seamounts[a] Islands[a,b] Open ocean[b]		_		Islands[a] Seamounts[a] Open ocean[b]	

al. 2006). However, it differs from the ichthyoneuston communities of St. Paul's Rocks (Macedo-Soares et al. 2012), the Fernando de Noronha Chain and the North Brazilian Chain (Lessa et al. 1999) likely due to sampling depth and the specificity of the ichthyoplankton compartiment targeted by these studies. Only the family Holocentridae has not been reported among the most abundant reef taxa of the VTC and adjacent areas (Ekau et al. 1999; Nonaka et al. 2000; Bonecker et al. 2006). The seasonal variation observed in abundance of reef taxa is consistent with the reproductive season of the respective taxa (Jones et al. 2006; Kelly 2006; Richards et al. 2006a, 2006b).

Seamounts cause deviations of flow that may result in upwelling currents, vortices, and Taylor cones/columns, which can lead nutrients, and possibly organisms, from the deep ocean toward the surface, promoting increased primary productivity and help to retain water masses over the top of seamount summit (White and Mohn 2002). Using numerical models, Lemos (2014) detected Taylor cones/columns above the summits of Vitória, Jaseur and Davis seamounts. These phenomena may contribute to the greater density of ichthyoplankton on seamounts compared to open ocean (Bonecker et al. 1992; Rezende et al. 2006; Table 2) and can extend to 30 km into the surrounding waters (Dower and Mackas 1996). Specifically, the high density of reef taxa could be related, among other factors, to their ability to remain on the reef through horizontal and vertical swimming oriented by smell, hearing and vision (Leis 2007).

Distance is an important biogeographical factor for, both, terrestrial and aquatic species. For example, the richness of terrestrial taxa on islands often decreases with distance from the nearest mainland (MacArthur and Wilson 1967), the diversity of pelagic fish species decreases with distance from seamounts (Morato et al. 2010) and the density of larvae of topographically associated species decreases with increasing distance of seamount from larger land masses (Boehlert and Mundy 1993). However, the density pattern was not observed in this study ($P>0.05$ for the position according to the distance from the continental shelf). Nevertheless, the first seamount of the chain, Vitória, showed the highest density in both summer and winter and, also, the second-highest (in summer) or highest (in winter) number of reef taxa. Besides its proximity to mainland, its large summit area extent probably enables higher recruitment from the coast, a higher diversity of environments (H.T. Pinheiro and E.F. Mazzei, comm. pers.) and therefore a higher richness of fish (MacArthur and Wilson 1967), acting as the first link between populations of the Brazilian coast, seamounts and remote islands.

Davis had the highest number of reef taxa in winter and the second highest density for reef taxa in both seasons (Figures 2 and 3). This seamount is characterized by its high structural complexity of large reefs (Jean-Christophe Joyeux, obs. pers.) and its ability to shelter a large number of species (Pinheiro et al. 2014). The seamount also has a truncated conical shape which favors the formation of a Taylor cone (or column, depending on water stratification; Lemos 2014) that promotes the retention of plankton and facilitates self-recruitment (Boehlert and Mundy 1993). The richness of reef fishes at the extremities of the chain, particularly remarkable at its eastern end (Figure 3), may be a result of the higher number of habitats available. The islands of Trindade and Martin Vaz are the only emerged locations of the chain. Therefore, they possess habitable depth ranges that are absent in the seamounts and that allow the persistence and self-recruitment of shallow-water species, including those of the intertidal zone. Currently, the VTC does not appear to act as stepping-stones for dispersal of shallow-water species (Simon et al. 2013), but the colonization of Trindade and Martin Vaz may have been facilitated by a process of stepping-stones during the Pleistocene glaciations. With the sea level 120 m below the current sea level, all seamounts were emerged during the last glacial maximum (e.g., Thomas et al. 2009) and therefore contained shallow-water habitat propitious to the settlement of these species (Simon et al. 2013; Macieira et al. 2015).

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