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Final Report

LONG-TERM PATTERNS OF DIVERSITY AND ABUNDANCE IN AN EASTERN PACIFIC REEF FISH ASSEMBLAGE: REEF FISH RESPONSE TO CORAL RECOVERY

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ABSTRACT

Discerning climatic impacts from other sources of variability (natural and anthropogenic) on systems as complex as coral reef communities requires multi-decadal datasets on a wide range of species. This project examines an eastern Pacific fish assemblage associated with a 2.5 hectare coral reef located within the boundaries of Coiba National Park, Panama. From 1980 to 2010, consistent, quantitative coral reef and fish survey monitoring methods have been applied at Uva Island reef, which lies in area that has received virtually no fishing pressure or watershed development over the past 80 years. Concurrent coral and fish monitoring spanned the 1982-83 and 1997-98 El Niño (ENSO) disturbances, anomalous warming events that selectively killed reef-building corals. While no fish mortalities were observed at the time of the 1982-83 El Nino event, live coral cover was reduced to near 0% at Uva reef. From 1984 to 1990, live coral (*Pocillopora* spp.) cover was extremely low (< 5%), but demonstrated steady recovery to ~ 70% by 2006. By quantifying disturbance-related, long-term changes in coral reef resources and relating these to fish trophic group responses, several functional relationships became apparent. Over the entire study period, a total of 63 fish taxa were observed and reef fish density (all taxa combined) remained relatively stable. Fish diversity (taxonomic richness) increased significantly as coral cover rose from near 0% to 20-30% then demonstrated a decreasing trend to 70% cover. Reef herbivore densities showed a similar significant parabolic relationship with highest abundances at 20-30% coral cover. Benthic invertivores showed a significant asymptotic increase in density to about 10% live coral cover. Mixed diet feeders and facultative corallivores demonstrated significant linear trends with increasing coral cover, with the former trophic group decreasing and the latter increasing as recovery progressed. Piscivores and planktivores did not demonstrate significant variations in abundance with increasing coral cover. The varying responses of herbivore, invertivore, corallivore and mixed diet feeding guilds demonstrated strong associations with coral cover, likely reflecting changes in availability of trophic resources during reef recovery. Further monitoring combined with manipulative studies are clearly warranted to validate the correlative relationships revealed in the present study.

INTRODUCTION

Coral reefs often serve as focal points for a high diversity of ichthyofauna with varied habits. Fish utilization of reef resources varies widely, from transient species that move onto reefs intermittently during feeding forays, to species that are permanent residents as juveniles and/or adults. These fishes depend on reefs for shelter, food, nest sites and numerous other resources (see chapters in Sale 1991, 2002; Montgomery 2011). Major disturbances to coral reefs may cause migrations and increases in mortality and, therefore, serve as drivers of change in fish community composition and structure. Recent coral reef ecosystem decline on a global scale is demonstrating a negative impact on coral reef fish communities (Jones et al. 2004, Wilson et al. 2006, Graham et al. 2011). On smaller scales, several studies have examined the effects of tropical storms on reef fish communities in Hawaii (Walsh 1983) and Jamaica (Woodley et al.1981, Kaufman 1983), as well as extensive predation events by the crown-of-thorns sea star (*Acanthaster*) in Japanese (Sano et al. 1984) and Australian (Williams 1986) waters. Grove (1985) reported on the responses of some Galapagos fishes to the severe El Niño event of 1982-83, which virtually eliminated all reef-building corals in the Galapagos Islands (Robinson 1985), and Wellington and Victor (1986) examined the effect of El Niño-related coral mortality (Glynn 1983, 1984) on reef damselfish populations off Panama.

The 1982-83 El Niño event resulted in significant reductions of scleractinian corals (50-95% overall on numerous reefs) and corresponding increases in algal-covered reef substrates (Glynn 1990), changes in densities of epibenthic invertebrates (Glynn 1985, 1988) and population structure of endolithic bioeroders (Scott et al. 1988) leading to significant bioerosion and reduction of reef structural complexity (Eakin 1996, 2001; Reaka-Kudla et al. 1996). All of these changes have widespread implications for nektonic reef fish populations as changes in food availability and shelter may affect community composition, abundance, distribution and diversity.

The goal of this study was to gain insight into the nature of relationships between corals and their associated fish communities. Concurrent monitoring of live coral cover and fish assemblages at Uva reef over a 30-yr time span provided a rare opportunity to examine for sequence of changes fish community composition and structure, ostensibly in response to the steady increase in live coral cover that occurred since the 1982 El Niño disturbance. We examined the temporal trajectories of several aspects of the Uva reef fish community including: (1) taxonomic richness (i.e., number of different taxa per transect); and (2) total fish density (i.e., species combined); and (3) densities of each of five trophic groups (i.e., piscivores, herbivores, facultative corallivores, benthic invertivores, and mixed diet feeders. Next, we investigated the nature of correlation, if any, between coral cover and each of the above fish community metrics by fitting linear, parabolic and asymptotic regression models. Given that coral cover increased from < 2 to ~70 % over the study period, we were in a position to examine the fish data for consistency with several hypotheses that have been suggested in the literature. Among these were that corallivore and herbivore densities would be positively and negatively correlated, respectively, with coral cover, while fish diversity would peak at some intermediate level.

METHODS

Study site

All surveys were carried out at the Uva Island reef, centered at 7º48'46"N, 81º45'35"W in the Pacific Gulf of Chiriquí, Panamá. This reef is ca 2.5 ha in planar area and is situated in a sheltered, NW-facing embayment. The principal framework-building corals are ramose, pocilloporid species, mainly *Pocillopora damicornis* and *Pocillopora elegans*. The most abundant massive corals are *Gardineroseris planulata, Pavona clavus* and *Pavona varians*, which are most commonly present as large colonies (ca. 0.5-1.0 m diameter) on the lower reef slope or along the reef base. Five other zooxanthellate scleractinians and one hydrocoral (*Millepora*) species also occur on the reef, but these are relatively unimportant in terms of live surface cover. Further information on reef zonation and coral community structure at Uva Island before the 1982-83 ENSO event is available in Porter (1972, 1974) and Glynn (1973, 1974, 1976), and following the 1997-98 event in Eakin (1996, 2001), Glynn and Maté (1997), Glynn et al. (2001), and Maté (2003).

Coral monitoring

Assessment of coral cover on the Uva reef began in 1974 (Glynn 1976) and has continued to 2010. This was accomplished by chain transects and by sampling fixed 1 m^2 plots (n = 10) as well as a single 4 x 5 m^2 plot bordering the fish transects. The 4 x 5 m plot was established by R.H. Richmond immediately following the 1982-83 ENSO event when coral cover on the fore-reef was reduced to near-zero values. For this study, percent coral cover was determined only from the 4 x 5 m fixed plot. Benthic composition of 1 m^2 sections were drawn by divers underwater and then digitized in the lab using a flatbed scanner, Adobe Photoshop and ImageJ software. Percent coral cover was determined by dividing the number of pixels representing coral within a quadrat by the total number of pixels in that quadrat. For each year, all 20 1 m^2 quadrats within the 4 x 5 m plot were averaged to determine the total mean percent coral cover.

Fish monitoring

Fish species numbers and abundances were quantified via snorkeling along the NW (seaward) side of the Uva Island patch reef. The surveys were conducted along 20 x 40 m transects with the longest axis oriented in the NW-SE direction, i.e., along the depth gradient and perpendicular to the zonation of fore-reef corals. The shallow ends of the transects were located in abundant pocilloporid growth (with scattered reef frame blocks) of relatively high relief; the central sections were dominated by live stands of *Pocillopora* spp. of low relief; the deep ends contained mostly coral rubble with a few isolated patches of massive corals. These substrate zonation patterns characterized the transect areas when sampling was first conducted. Live coral cover returned gradually from near complete loss following the 1982-83 El Niño to pre-disturbance levels as of March 2010. All surveys were conducted at or near high tide. At this time, the shallow ends of the transects were 3-4 m deep and their deep ends 5-7 m. The spring tidal range in this area is 3.3 m. Surveys were conducted when the lateral visibility was ≥10 m. Snorkeling was carried out along the major axis of transects in a straight line pattern to permit a clear view of the transect boundaries. Fish counts were made by snorkeling slowly, avoiding quick movements or splashing, down the long axis of the transect. Species and abundance of individuals ≥ 15 cm total body length present within the transects were recorded on a slate. Sampling time was standardized at 8 minutes per transect (per 800 m^2). The sides of adjacent transects were separated by 3 m and the time interval between successive visual sampling was approximately 5 minutes. Fishes did not seem to be either attracted or repelled by the observer.

Trophic group assignments

For the purposes of this study, trophic groups were defined as follows: piscivores, consuming primarily or exclusively living fishes; planktivores, consuming primarily or exclusively plankton; herbivores, consuming primarily benthic algae; corallivores, consuming primarily scleractinian corals; mixed diet feeders, exhibiting broad diets not easily classified into a single food category; and benthic invertivores, consuming primarily motile benthic invertebrates.

Assignment of fishes to trophic groups (Table 1) was determined from feeding observations and gut analyses conducted on coral reefs in Panama over a 15 year period and from existing literature. Feeding observations were made on two occasions (20-25 June 1975; 14-15 May 1979) on the Uva reef with scuba in 5 x 5 meter study plots located on the reef flat, upper fore-reef slope and reef base. Diurnal feeding activities were recorded on slates continuously for one hour by an observer at the outside corner of the study plot. Observations were- conducted at high and low water, in the early morning (0600-0730), midday (1000-1400), late afternoon (1700-1800), and at night (1900-2100). At night a flashlight was used for 10 seconds at 2 minute intervals to illuminate the plot, thereby totaling 5 minutes (per hour) of intermittent observations. Additionally, most species feeding behaviors were supplemented by many hours of observations in other studies in Panama (e.g., Glynn et al. 1972, Glynn 1974, 1984, 1985).

Data analysis

To reduce problems of non-normality and heteroscedasticity, total fish and trophic group density data were $\log_e$-transformed prior to statistical analyses; coral cover percentages (proportions) were arcsine-transformed following Sokal and Rohlf (1981). Taxonomic richness (fish diversity) values did not require transformation. Temporal pattern and coral-fish correlation analyses were based on mean levels per season-year combination (e.g., dry-2000, wet-2000, dry-2001, etc.). To examine their temporal trajectories, mean taxonomic richness (fish diversity), total fish density (species combined) and density values for each guild (expressed per 800 m^2) were plotted in chronological sequence. To examine for linear, parabolic or asymptotic relationships between coral cover and each fish community metric, ordinary least squares and nonlinear regression was performed using SAS (1990) statistical software. The linear, parabolic and asymptotic regression models, respectively, took the form $y=b_0 +b_1$, $y=b_0 + b_1x + b_2x$, and $y=b_0(1-\exp(x^*-b_1))$, where y=fish metric, x=coral cover and b_0-b_2 are the estimated regression coefficients. Model goodness-of-fit was first judged on the basis of its statistical significance ($p<0.05$), and then according to its R^2 and/or Akaike Information Criterion (AIC) value.

RESULTS

Coral cover

Coral cover assessed in 1984, one year after the ENSO bleaching event, was 0% (Figure 1). By 1994 and 1995, *Pocillopora* spp. corals recruited to the study plot, and increased to ~20% cover by 1997. In 2010, 27 years after the bleaching/mortality event, pocilloporid cover was ~70%, similar to pre-disturbance abundance. Nearly all of the coral belonged to *Pocillopora* spp.

with <1% contributed by *Porites* and *Pavona*. From 2002 on, *Pocillopora* cover was continuous with vertical growth and reef framework development in certain areas.

Fish community

A total of 224 transects were sampled over the 30-year monitoring period (1980-2010). Fishes recorded during this period are listed in rank order of the total number of individuals observed and assigned trophic groups in Table 1. Abundance details for each species observed are presented in the Appendix. Of the 63 taxa, 58 were identified to species, three to genus and two to the family level. It is likely that the *Lutjanus* sp. and Carangidae sp. taxonomic groups were each represented by more than one species. All 22 of the numerically-dominant ($n \geq 40$ individuals) taxa were identified to species. The two predominant trophic groups were mixed diet feeders (MDF) and benthic invertivores (BIN), which consisted of 21 and 20 member species, respectively. Some species ranking high in abundance, e.g. *Lutjanus viridis* and *Paranthias colonus*, typically occurred in large schools that were often absent during sampling periods. However, several abundant species, such as *Sufflamen verres*, *Arothron meleagris*, *Holacanthus passer* and *Scarus rubroviolaceus*, were consistently present during all sampling dates over the course of the study.

Regression statistics describing the shape, fit and significance of relationships between fish diversity (species richness) and abundance (species combined and by trophic group) against coral cover are shown in Table 2. Reef fish community abundance (all taxa pooled) was relatively stable over the study period (Figure 2A) with mean density ranging from 20 to 50 individuals per transect (800 m^2). Mean taxonomic richness (Figure 2B) ranged between 6 and 9 taxa from 1980 to 2010. The temporal trend for taxonomic richness, was one of gentle increase until about 2001, followed by gentle decline over the next nine years. While reef fish community densities were relatively stable regardless of coral abundance (Figure 3A), taxonomic richness demonstrated a significant ($p = 0.0037$) parabolic relationship with coral cover (Figure 3B). Relatively low mean values of 6 to 8 taxa per transect were observed at low and high coral cover and maximum richness values of 8-10 between 20-40% coral cover (Figure 3B).

Trophic groups

Mean trophic group densities varied widely over time, with trends of increase, decrease or no change depending on the group under scrutiny (Figure 4). Densities of piscivores (Figure 5A) and planktivores (Figure 5B) appeared uncorrelated with live coral cover; however, this was not the case for densities of the four remaining trophic groups (Figure 5C-F). Herbivores (Scaridae and Acanthuridae) showed a significant ($p = 0.0364$) parabolic relationship with maximum densities at 20-30% live coral cover (Figure 5C). Two significant, but opposite, linear relationships were observed in faculative corallivore (Figure 5D, $p = 0.0001$) and mixed diet feeding (Figure 5E, $p = 0.0227$) trophic groups. Corallivores (predominantly *Arothron meleagris*) increased in density with increasing coral cover, while mixed diet feeders (predominantly *Lutjanus* spp. and *Holacanthus passer*) demonstrated declines in density at high coral abundance. Members of the benthic invertivore group (predominantly the balistid *Sufflamen verres*) demonstrated a highly significant (Figure 5F, $p = 0.0004$) asymptotic increase in density with increasing coral cover. Mean density increased from about 7 indiv. at 0% cover and ranged between 12 to 15 indiv. from 10 to 70% coral cover.

DISCUSSION

Patterns in community diversity

Despite a severe reduction in live coral cover following the 1982-83 ENSO bleaching event, overall coral fish community densities fluctuated relatively little over the 30-year sampling period. Taxonomic richness, however, increased as live coral cover rose from 0% to about 25%, but then fell at yet higher coral cover values. A possible explanation for this pattern is that fish diversity directly tracked the diversity of food and shelter resources (e.g., algal turfs, coral-associated metazoans, shelter sites, Leviten and Kohn 1980), which also followed this parabolic trend. Another potentially major event that could have affected fish diversity was the establishment of the Coiba National Park in 1991 (Maté 2003). This marine protected area (MPA) encompasses 270,125 ha, including the Uva Island coral reef. As the ten year period following the Park's establishment was one of steady fish diversity increase, it is possible that heightened custodial police presence associated with the National Park contributed to the diversity rise. However, unless there followed a reduction in police presence post-2001, it seems more likely ecological rather than anthropogenic factors were at play in reducing fish diversity over the last 10 years of record.

Trophic group abundances

Drastic changes in fish species composition, abundance and diversity were generally lacking in this long-term study, which spanned three decades and two extreme disturbance events. However, detailed analyses revealed significant changes in fish densities of particular trophic groups as they relate to several essential resources associated with the coral habitat under investigation. Numerous studies have shown that obligate corallivores generally die within weeks of the disappearance of their coral prey (e.g., Spalding and Jarvis 1998, Shibuno et al. 1999, 2002, Kokita and Nakazono 2001, and Sano 2004). This has been demonstrated for species in the families Gobiidae, Pomacentridae, Monacanthidae, and Chaetodontidae. The facultative corallivore *Arothron meleagris*, the guinea fowl puffer, showed relatively low abundances soon after coral cover loss, but then increased in abundance to 20% live coral cover and remained at 4 to 5 individuals per transect for several years. This increase was presumably due to a recovering food source, which at the Uva reef was *Pocillopora* spp (Glynn 2008). It is likely that the low abundances were influenced in part by the movement of puffers off the reef to communities of *Psammocora stellata,* a prey species they also consume (Guzman and Robertson 1989). Since *A. meleagris* is territorial, population densities do not exceed 50 to 60 individuals ha^{-1}.

Fish herbivore densities also showed a similar significant parabolic relationship with increasing coral cover, which may reflect diminishing algal-covered substrates as coral recruitment and growth progressed beyond about 30% live cover. The less pronounced linear decline in mixed diet feeder densities with increasing coral cover could have resulted from a greater sheltering effect of potential prey. As pocilloporid coral cover increased higher than 50%, colonies began to fuse forming interlocking frameworks and increased topographic complexity, thus creating shelter sites for motile invertebrates and small fishes.

The significant declines in density of herbivores and mixed diet feeders with increasing coral cover could possibly have been due to the movement of these fishes to different reef zones to increase their feeding efficiency. Unlike the time-lag response in reef fish abundances observed in the Indian Ocean, which was brought about by significant declines in the structural complexity and shelter sites for fish recruits (Graham et al. 2007, this hypothesized effect does not seem likely on the Uva reef). Topographic complexity at the Uva reef site varied greatly among zones, but did not show a significant overall decline (Eakin 2001).

A strong relationship between declining fish abundances and reef framework loss has been shown following *Acanthaster* and bleaching disturbances. Loss of three-dimensional structures has increased mortality due to loss of shelter and elevated predation. At Uva, variations in fish abundances are due more to trophic interactions and not loss of structure. Initially there were high rates of bioerosion, but this declined as sea urchin populations declined. Much of framework is dead, but still largely intact. A large part of recovery occurred on summits of dead reef frames.

An increase in the abundance of benthic invertivores over the post-ENSO 10-year period (1984-1994) corresponded closely with the recovery of *Pocillopora* and the increasing availability of coral-associated prey. Both facultative and obligate invertebrates associated with live coral undergo sudden high mortality with the bleaching and death of their hosts (Glynn et al. 1985, Caley et al. 2001, Baker et al. 2008). This mortality is due to the loss of host-generated trophic resources (mucus, coral tissue, zooxanthellae, interalia), the emigration of invertebrates from corals (Castro 1978), and their increasing susceptibility to predation in bleached colonies (Coker et al 2009). This study has demonstrated that the Uva fish invertivore guild begins to recover when live corals reach about 10% cover.

Globally numerous coral reefs are in a dramatic state of decline (Gardner et al. 2003; Hoegh-Guldberg et al. 2007; Baker et al. 2008; Eakin et al. 2009). Many of these reefs are in varying stages of erosion, with significant loss of framework structures due to bioerosion and low coral recruitment. This has led to noticeable declines in topographic complexity with accompanying negative effects on fish communities (Wilson et al. 2006). Long-term monitoring of the Uva reef in Panama demonstrated significant erosion by echinoids in the few years immediately following ENSO-induced coral mortality. With the decline of echinoid abundances in the mid-1990s to the present (Eakin 2001; Wellington and Glynn 2007) most pre-1983 framework structures remained intact with rapid recruitment and growth of *Pocillopora* corals. This reef recovery has probably contributed to the relative stability of the Uva reef fish communities. The availability of off-reef resources may also have helped stabilize the overall abundance of reef fishes.

This study is unique in that it examines the longest running reef fish survey ever conducted in eastern Pacific waters. By virtue of its long duration, several patterns suggestive of cause-and-effect relationships between fishes and coral-associated resources (i.e., food and shelter) were revealed. Clearly, additional fish and coral monitoring at this site and others in the region are warranted to test for consistency in patterns within and among eastern Pacific reefs. However, long-term manipulative studies are also needed to test the correlative relationships that emerged here and to pinpoint more precisely the nature and magnitude of resource dependency among reef-associated fishes. This will be important for advancing our understanding of how natural and anthropogenic factors will interact to shape reef fish communities in future decades.

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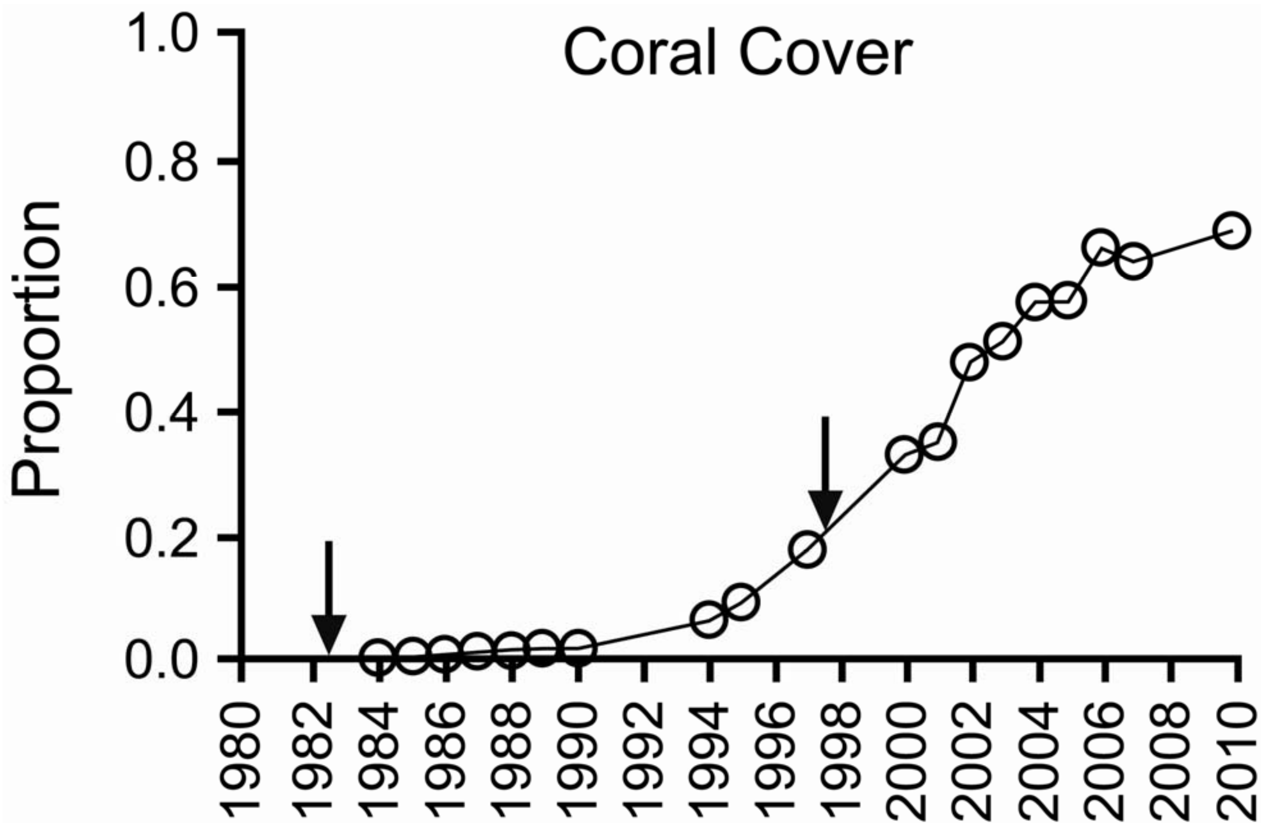


Figure 1. Variation in coral cover at the Uva Island reef from 1984 to 2010. Vertical arrows denote El Niño thermal anomaly events.

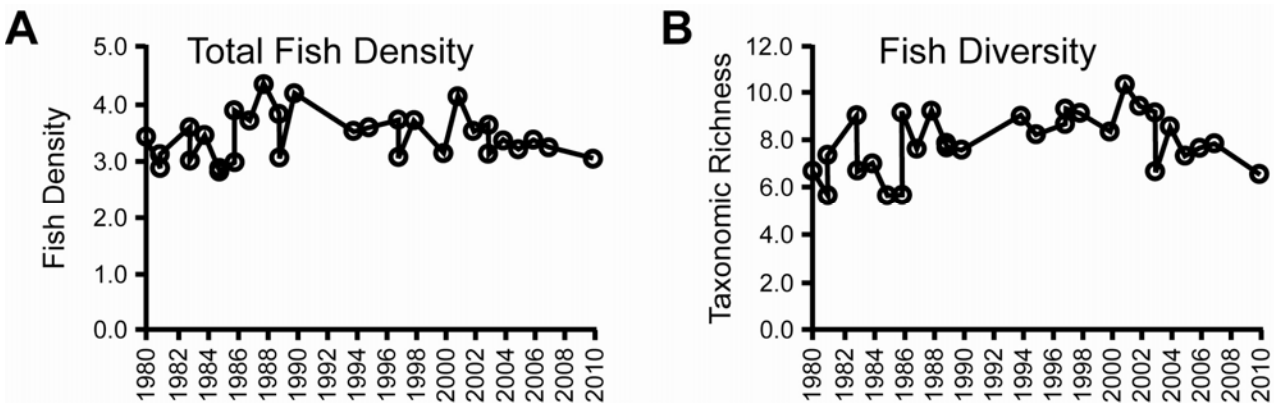


Figure 2. (A) Variation in total fish density (mean number of fishes per 800 m^2 transect) and (B) diversity (total number of species per transect) at the Uva Island reef from 1980 to 2010. Fish density data is $\log_e$ transformed.

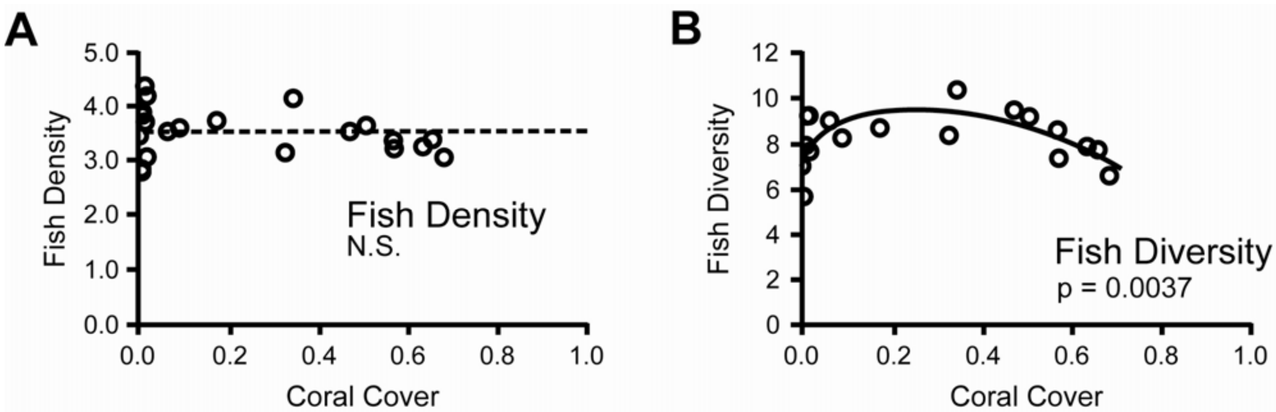


Figure 3. Non-significant linear correlation between total fish density and coral cover (A) and significant parabolic correlation ($p = 0.0037$) between total community richness and coral cover (B). Fish density is $\log_e$ transformed and percent coral cover is back calculated from arcsine transformations.

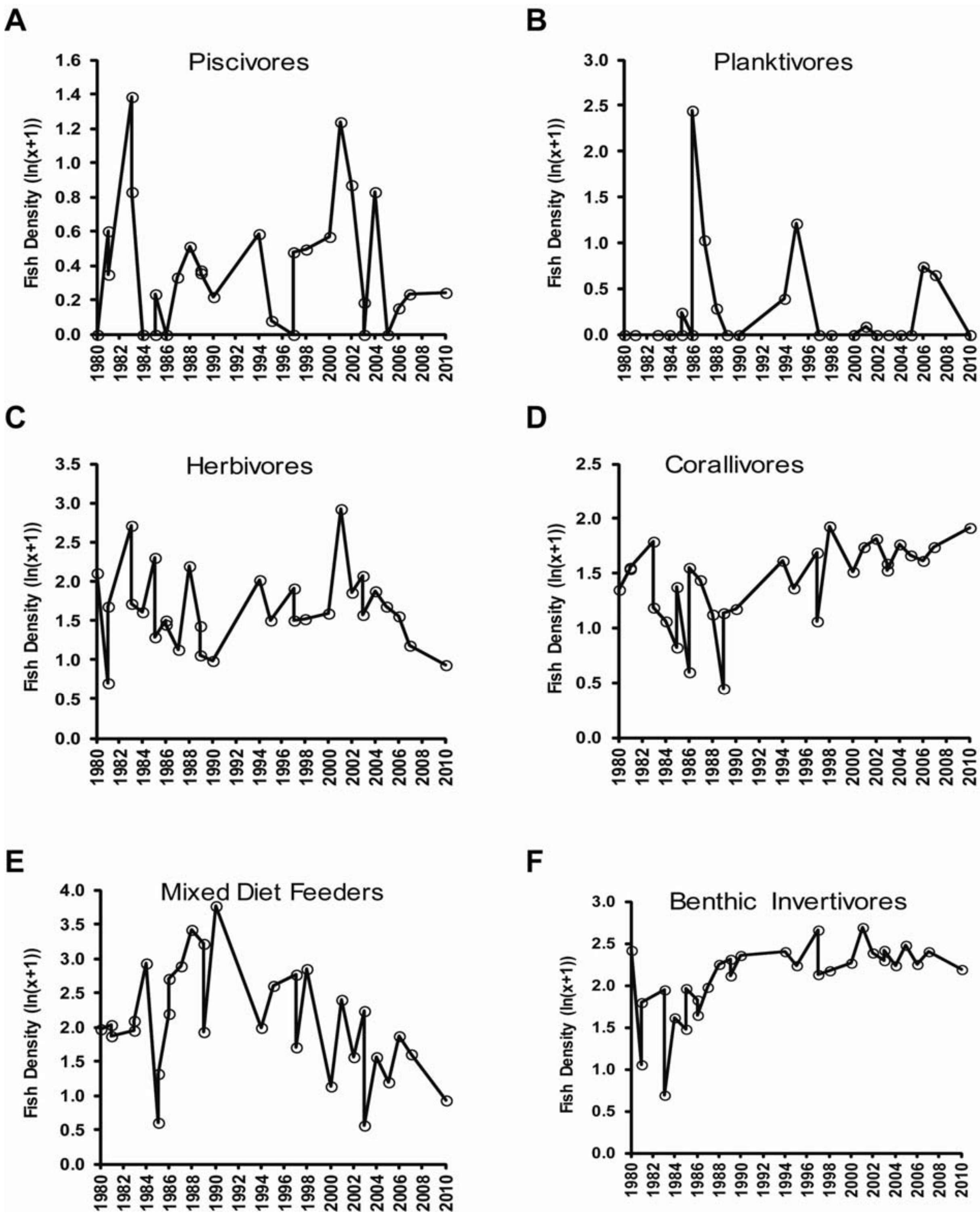


Figure 4. Changes in yearly mean fish trophic group density from 1980 to 2010. Values are $\log_e$ transformed.

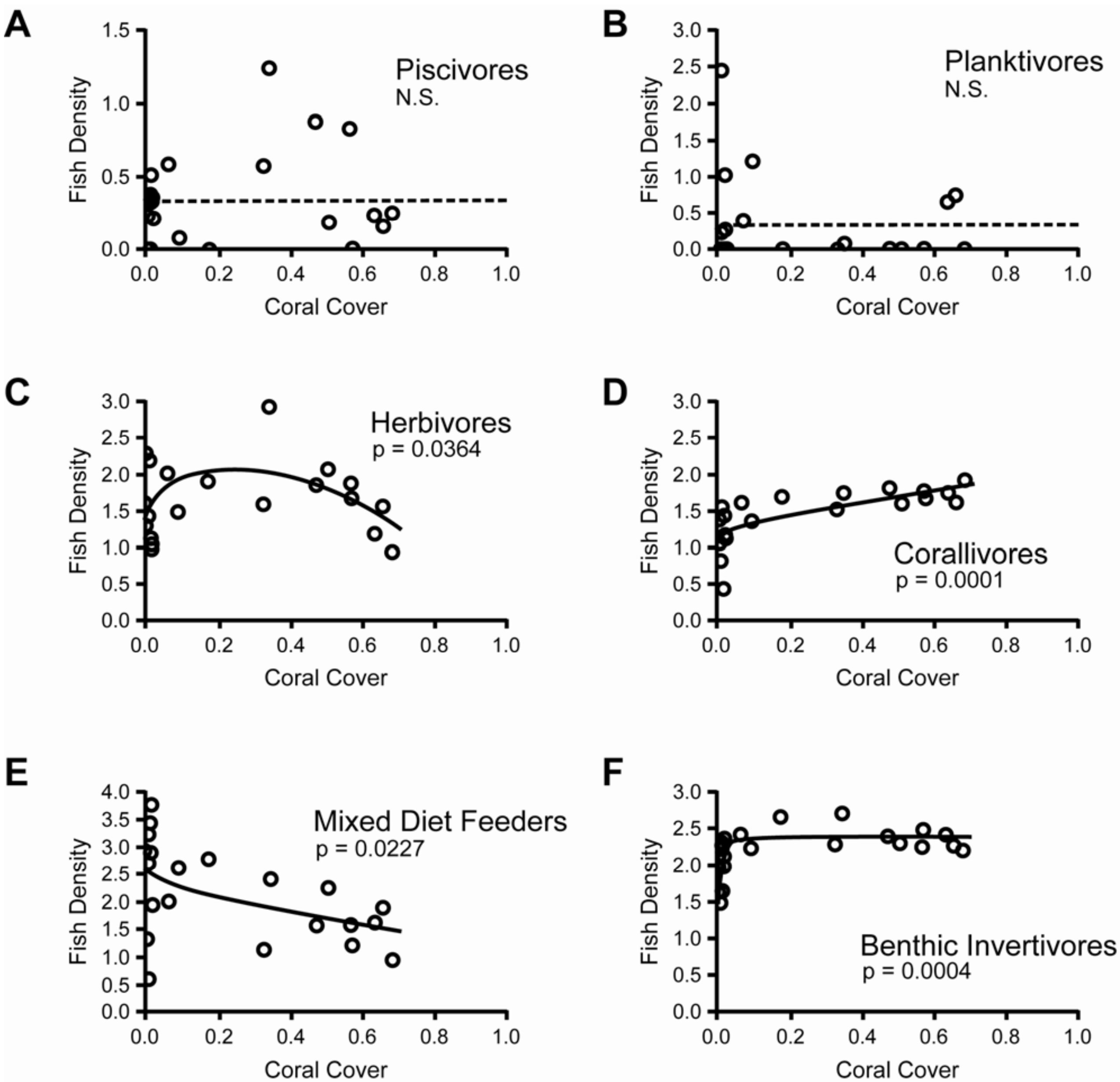


Figure 5. Correlation between fish trophic group density and percent coral cover. Fish densities are $\log_e$ transformed and percent coral cover is arcsine transformed. A, B are not significant. C shows significant parabolic correlation, D,E are linear correlation and F is asymptotic.

Species	Family	Number	%Occurence	Mean Density	Trophic Group
Lutjanus viridis	Lutjanidae	2265	17.0	10.1	MDF[1,2]
Sufflamen verres	Balistidae	1497	98.7	6.7	BIN[1,2,8]
Arothron meleagris	Tetraodontidae	743	87.5	3.3	FAC[2,4,6,8]
Holacanthus passer	Pomacanthidae	667	80.4	3.0	MDF[1,2,8]
Scarus rubroviolaceus	Scaridae	567	79.5	2.5	HRB[1,2,5]
Lutjanus argentiventris	Lutjanidae	544	36.2	2.4	MDF[1,7,8]
Scarus ghobban	Scaridae	370	49.1	1.7	HRB[1,2,3]
Paranthias colonus	Serranidae	210	13.4	0.9	PLK[1,2,3,8]
Acanthurus xanthopterus	Acanthuridae	195	26.8	0.9	HRB[1,2,3,6]
Johnrandallia nigrirostris	Chaetodontidae	152	34.8	0.7	FAC[2]
Fistularia commersonni	Fistulariidae	149	20.5	0.7	PIS[1,2,8]
Lutjanus guttatus	Lutjanidae	136	7.1	0.6	MDF[1]
Caranx caballus	Carangidae	123	1.3	0.5	PIS[3]
Novaculichthys taeniourus	Labridae	121	31.3	0.5	BIN[1,6]
Arothron hispidus	Tetraodontidae	103	33.0	0.5	BIN[1,2,6]
Cephalopholis panamensis	Serranidae	83	25.9	0.4	MDF[1,8]
Mulloidichthys dentatus	Mullidae	66	2.7	0.3	BIN[1,8]
Thalassoma grammaticum	Labridae	66	18.3	0.3	BIN[1]
Chaetodon humeralis	Chaetodontidae	59	12.1	0.3	MDF[1]
Tylosurus crocodilus fodiator	Belonidae	50	4.9	0.2	MDF[1]
Haemulon steindachneri	Haemulidae	47	1.8	0.2	MDF[1,3]
Pseudobalistes naufragium	Balistidae	41	12.5	0.2	BIN[1,2]
Lutjanus sp.	Lutjanidae	38	4.0	0.2	MDF[1,2,6]
Acanthurus nigricans	Acanthuridae	36	12.5	0.2	HRB[1,2,3]
Euleptorhamphus viridis	Hemiramphidae	35	2.7	0.2	PLK[1]
Zanclus cornutus	Zanclidae	32	8.5	0.1	FAC[2]
Bodianus diplotaenia	Labridae	29	10.7	0.1	BIN[1,2,3,8]
Seriola rivoliana	Carangidae	27	5.4	0.1	PIS[1,2]
Scarus perrico	Scaridae	23	7.1	0.1	HRB[1,2,8]
Diodon holocanthus	Diodontidae	21	8.0	0.1	BIN[1,2,5]
Ctenochaetus marginatus	Acanthuridae	20	4.0	0.1	HRB[2]
Carangidae sp.	Carangidae	17	2.7	0.1	MDF[2]
Pomacanthus zonipectus	Pomacanthidae	14	5.8	0.1	BIN[1,8]
Halichoeres nicholsi	Labridae	13	5.8	0.1	BIN[1,2,8]
Belonidae sp.	Belonidae	11	0.9	<0.1	PIS[1]
Haemulon maculicauda	Haemulidae	11	0.4	<0.1	BIN[1]
Scarus compressus	Scaridae	10	1.3	<0.1	HRB[1]
Platybelone argalus	Belonidae	9	0.9	<0.1	MDF[1]

Caranx melampygus	Carangidae	8	2.2	<0.1	PIS[2,6]
Gnathanodon speciosus	Carangidae	8	1.3	<0.1	BIN[1,2]
Acanthurus triostegus	Acanthuridae	7	1.3	<0.1	HRB[1,2,3,6]
Epinephelus labriformis	Serranidae	7	3.1	<0.1	MDF[1,2,7,8]
Myripristis leiognathus	Holocentridae	7	1.3	<0.1	PLK[1,7]
Diodon hystrix	Diodontidae	6	2.2	<0.1	BIN[1,2,5,6]
Tylosurus sp.	Belonidae	6	0.4	<0.1	PIS[2]
Dermatolepis dermatolepis	Serranidae	5	1.8	<0.1	BIN[1]
Kyphosus analogous	Kyphosidae	5	1.3	<0.1	MDF[1,8]
Aluterus scriptus	Monacanthidae	2	0.4	<0.1	MDF[1]
Aulostomus chinensis	Aulostomidae	2	0.4	<0.1	MDF[1,5]
Elagatis bipinnulata	Carangidae	2	0.9	<0.1	MDF[1,6]
Halichoeres chierchiae	Labridae	2	0.9	<0.1	BIN[1,8]
Ostracion meleagris	Ostraciidae	2	0.9	<0.1	BIN[1,5,8]
Balistes polylepis	Balistidae	1	0.4	<0.1	BIN[1,2,7,8]
Dasyatis longus	Dasyatidae	1	0.4	<0.1	BIN[1]
Gymnothorax castaneus	Muraenidae	1	0.4	<0.1	MDF[1,8]
Gymnothorax undulatus	Muraenidae	1	0.4	<0.1	MDF[1]
Halichoeres semicinctus	Labridae	1	0.4	<0.1	BIN[1,8]
Kyphosus elegans	Kyphosidae	1	0.4	<0.1	MDF[1,2]
Lutjanus novemfasciatus	Lutjanidae	1	0.4	<0.1	MDF[1,8]
Scarus sp.	Scaridae	1	0.4	<0.1	HRB[2]
Scorpaena mystes	Scorpaenidae	1	0.4	<0.1	MDF[1,8]
Sectator ocyurus	Kyphosidae	1	0.4	<0.1	PLK[1]
Urobatis halleri	Urotrygonidae	1	0.4	<0.1	BIN[1]

Table 1. Listing of fish taxa observed during reef fish surveys. Acronyms refer to the following trophic groups: Benthic Invertivores (BIN), Facultative Corallivores (FAC), Herbivores (HRB), Mixed Diet Feeders (MDF), Piscivores (PIS), Planktivores (PLK). Superscripts indicate literature sources for trophic assignment (1=Robertson and Allen 2008; 2=Glynn pers. Obs; 3=Dominici-Arosemena and Wolff 2006; 4=Guzman and Robertson 1989; 5=Hobson 1974; 6=Hiatt and Strasburg 1960; 7=Hobson 1965; 8=Thomson et al. 2000).

Dependent Variable	Model	SSE	R^2	P-values	AIC	Best
Fish Density (species combined)	Linear	3.4135	0.051	0.325	-34.1527	None
	Parabolic	3.0091	0.1634	0.1373	-34.8003	
	Asymptotic	3.3829	N/A	N/A	-34.3416	
Species Richness	Linear	27.3729	0.0455	0.3534	9.565621	Parabolic
	Parabolic	15.3716	0.464	0.0037	-0.55198	
	Asymptotic	19.9969	N/A	N/A	2.972151	
Piscivores	Linear	2.0936	0.0577	0.2944	-44.4185	None
	Parabolic	1.7207	0.2255	0.0638	-46.5382	
	Asymptotic	1.9450	N/A	N/A	-45.9645	
Benthic Invertivores	Linear	1.4553	0.2713	0.0155	-52.0555	Asymptotic
	Parabolic	0.8416	0.5786	0.0004	-61.5554	
	Asymptotic	0.7500	N/A	N/A	-65.9763	
Herbivores	Linear	4.8427	0.0063	0.7327	-26.8079	Parabolic
	Parabolic	3.7721	0.226	0.0364	-30.0549	
	Asymptotic	4.8700	N/A	N/A	-26.69	
Facultative Corallivores	Linear	1.1937	0.5487	0.0001	-56.2161	Linear
	Parabolic	1.0851	0.5898	0.196	-56.2208	
	Asymptotic	1.3281	N/A	N/A	-53.9762	
Mixed Diet Feeders	Linear	11.4530	0.2445	0.0227	-8.73163	Linear
	Parabolic	11.0314	0.2723	0.4177	-7.51931	
	Asymptotic	15.1640	N/A	N/A	-2.83756	
Planktivores	Linear	7.0411	0.0417	0.3747	-18.948	None
	Parabolic	6.9704	0.0513	0.6742	-17.1599	
	Asymptotic	7.3342	N/A	N/A	-18.0915	

Table 2. Regression statistics describing the shape, fit and significance of relationships between fish diversity (species richness) and abundance (species combined and by trophic group) against coral cover.

APPENDIX

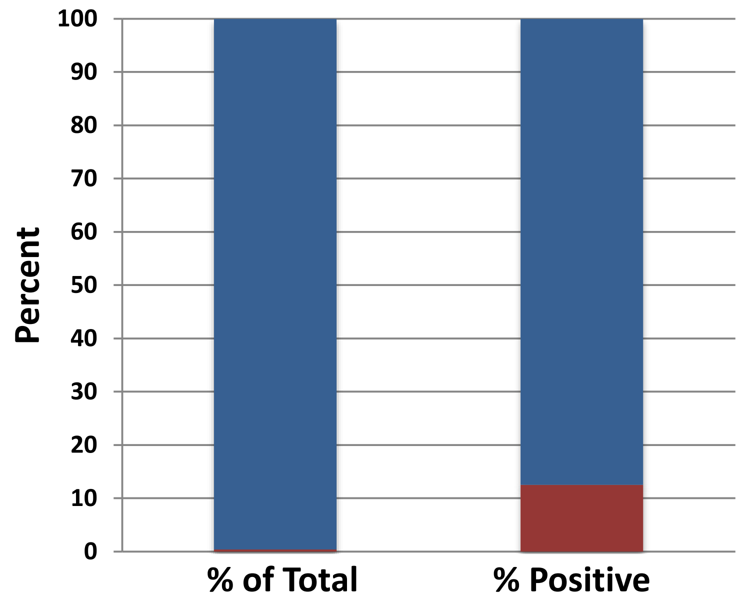
Abundance patterns for all fishes observed at Uva Island reef over the period of record (1980-2010). Fishes presented in alphabetical order with maximum size and trophic group designation. Summarized are species-specific results of 224, 800 m^2 visual belt-transect sampling. Shown in the top right panels is the proportion of all fishes that each species represents as well as the proportion of all visual transects that were positive for that species. Bottom panel shows species-specific distribution (per 800 m^2 transect) versus time, with wet and dry seasons indicated in red and blue, respectively. Gray shading indicates El Niño events.

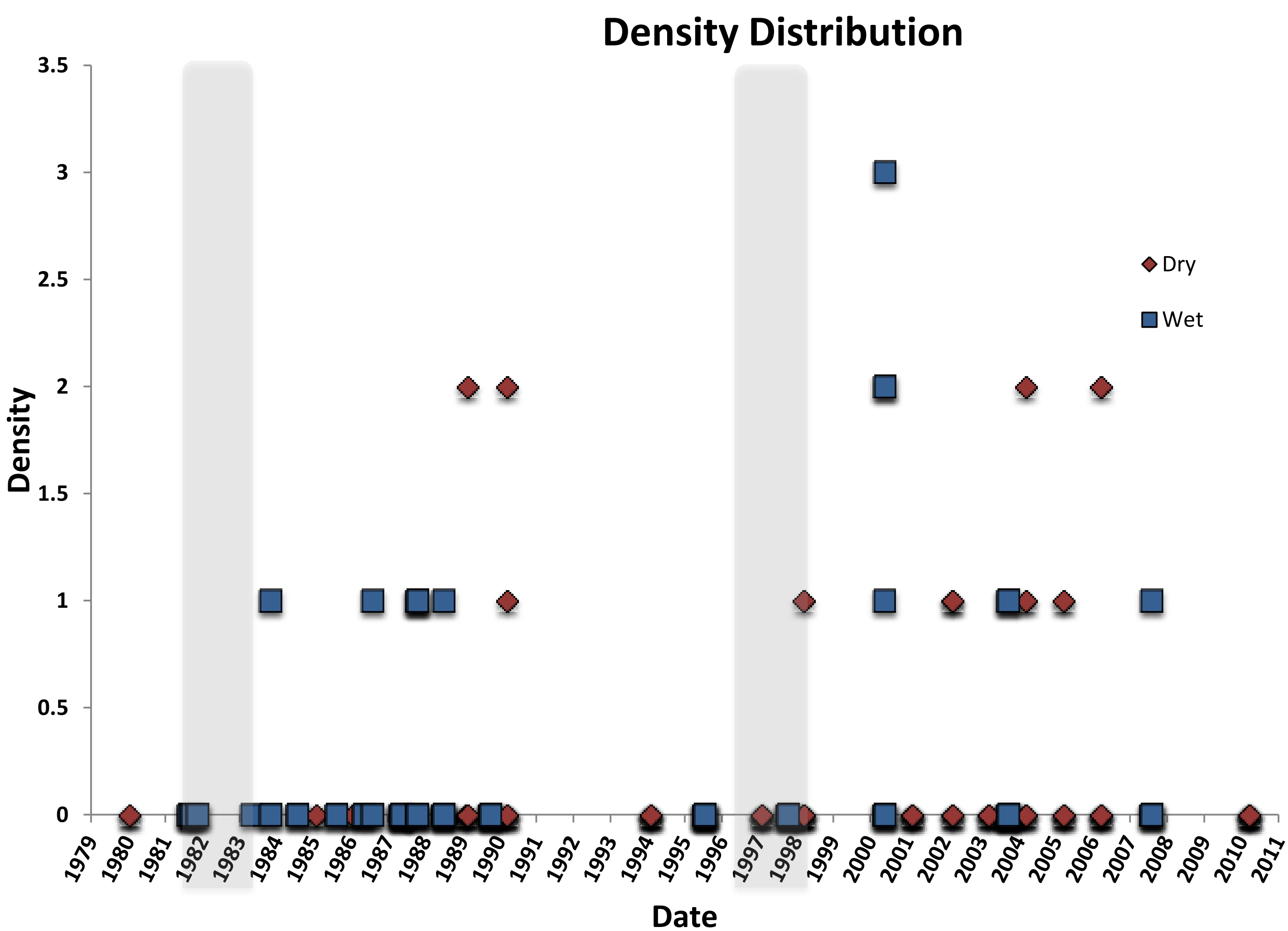
Acanthurus nigricans

Goldrimmed surgeonfish

Max. size: 22 cm

Trophic group: Herbivore



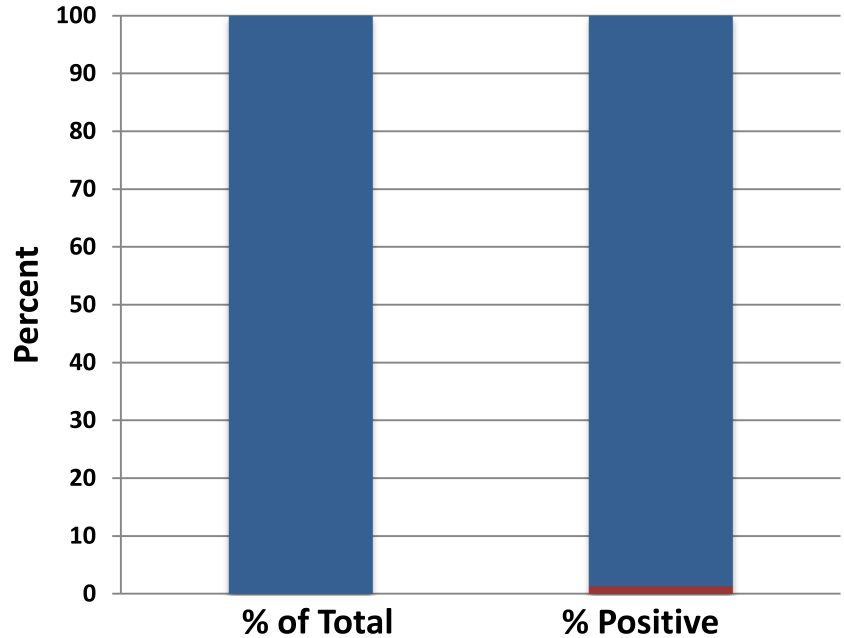


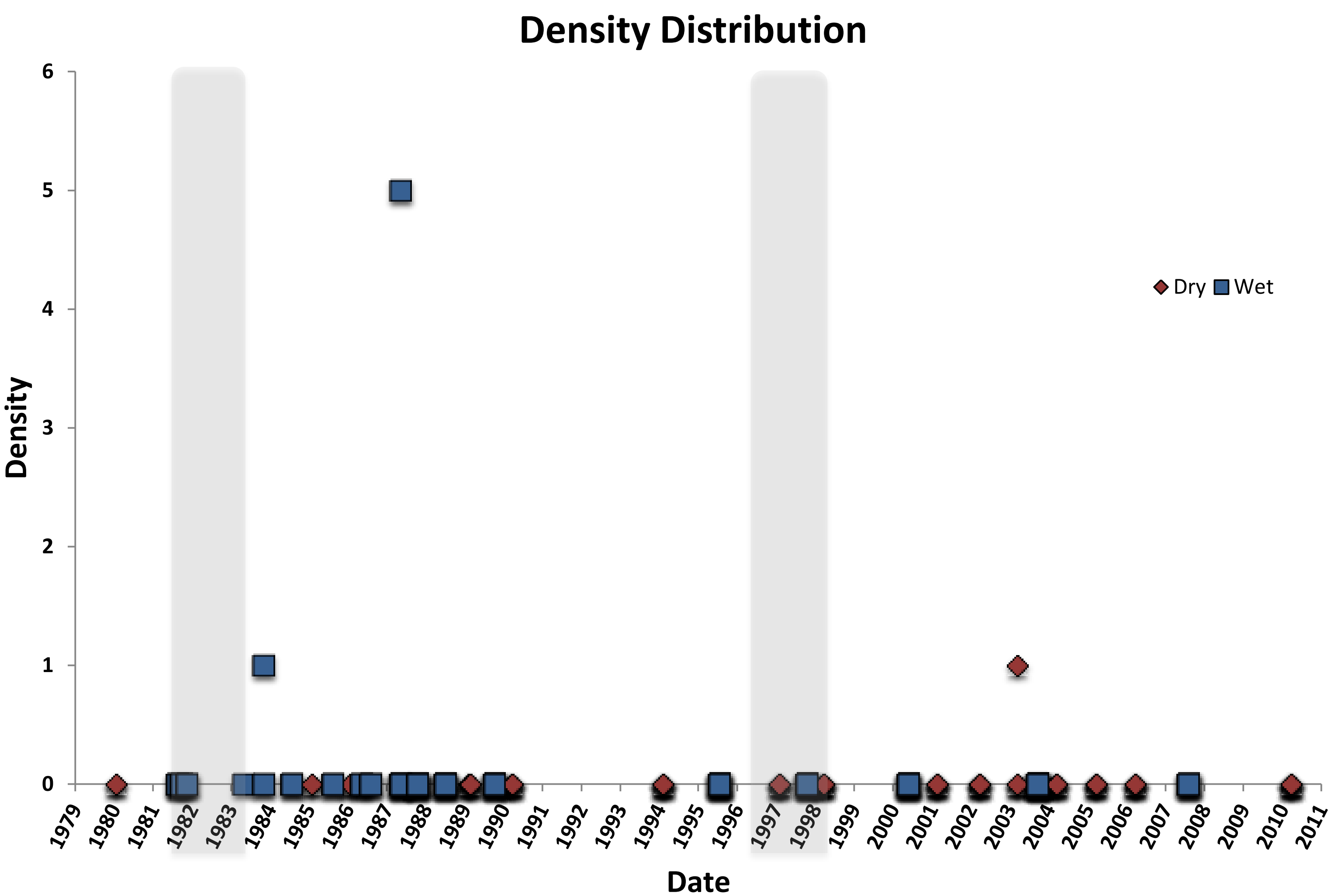
Acanthurus triostegus

Convict surgeonfish

Max. size: 27 cm

Trophic group: Herbivore



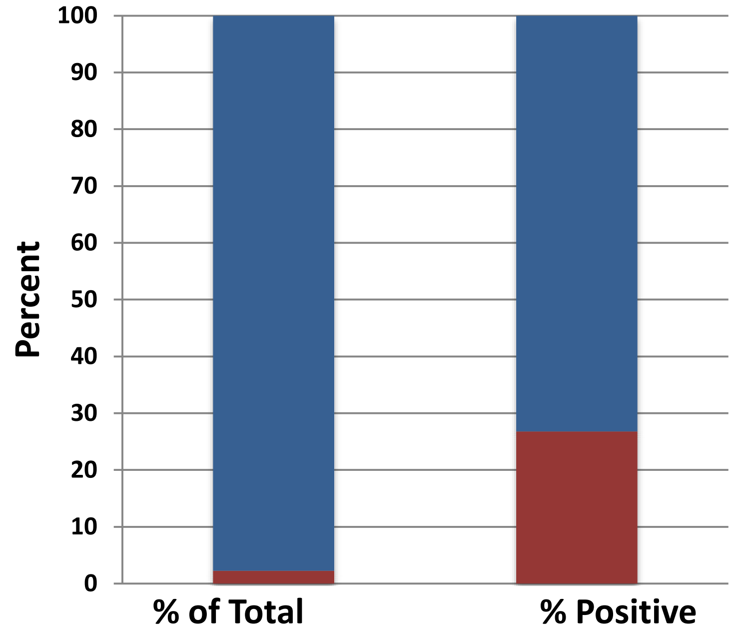


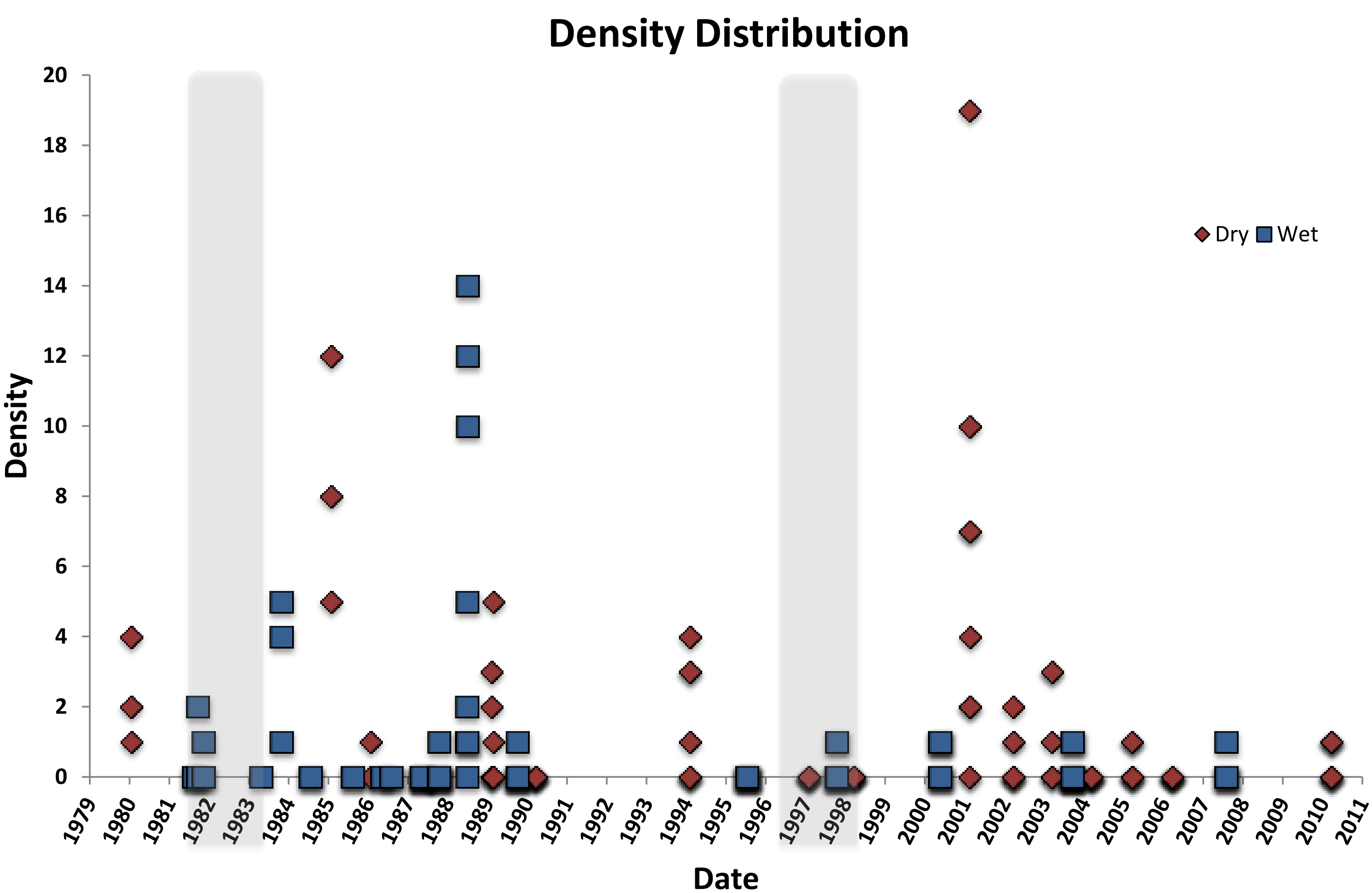
Acanthurus xanthopterus

Purple/yellow surgeonfish

Max. size: 70 cm

Trophic group: Herbivore



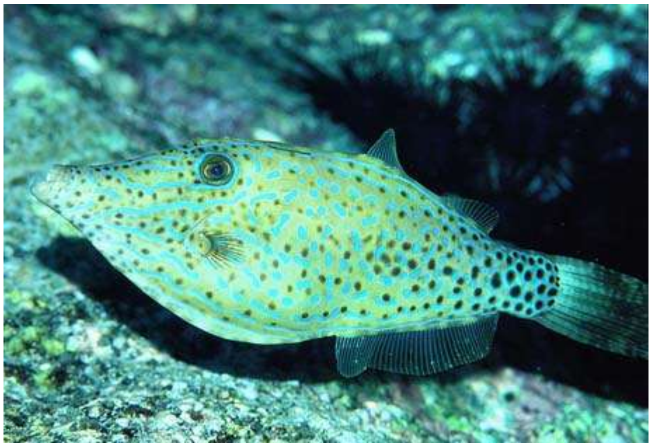


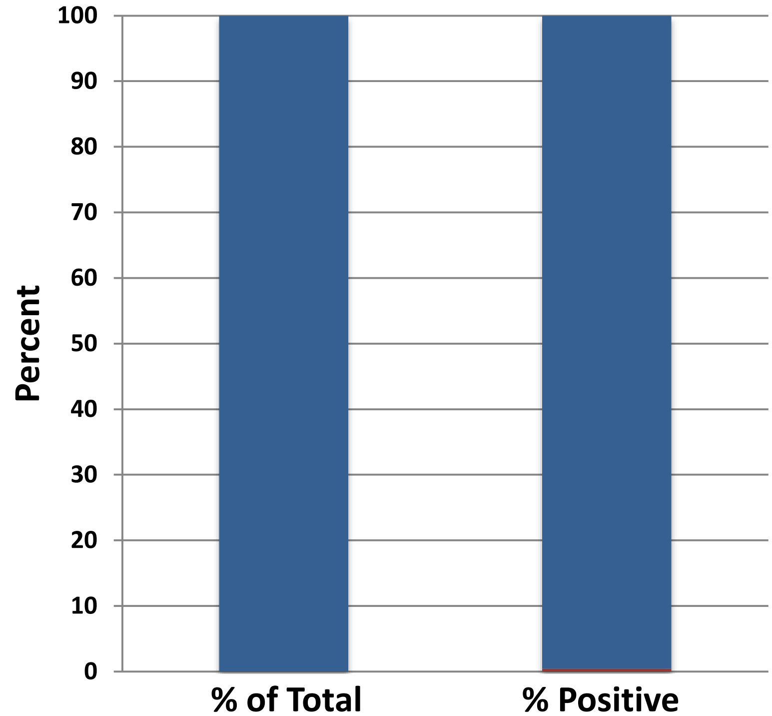
Aluterus scriptus

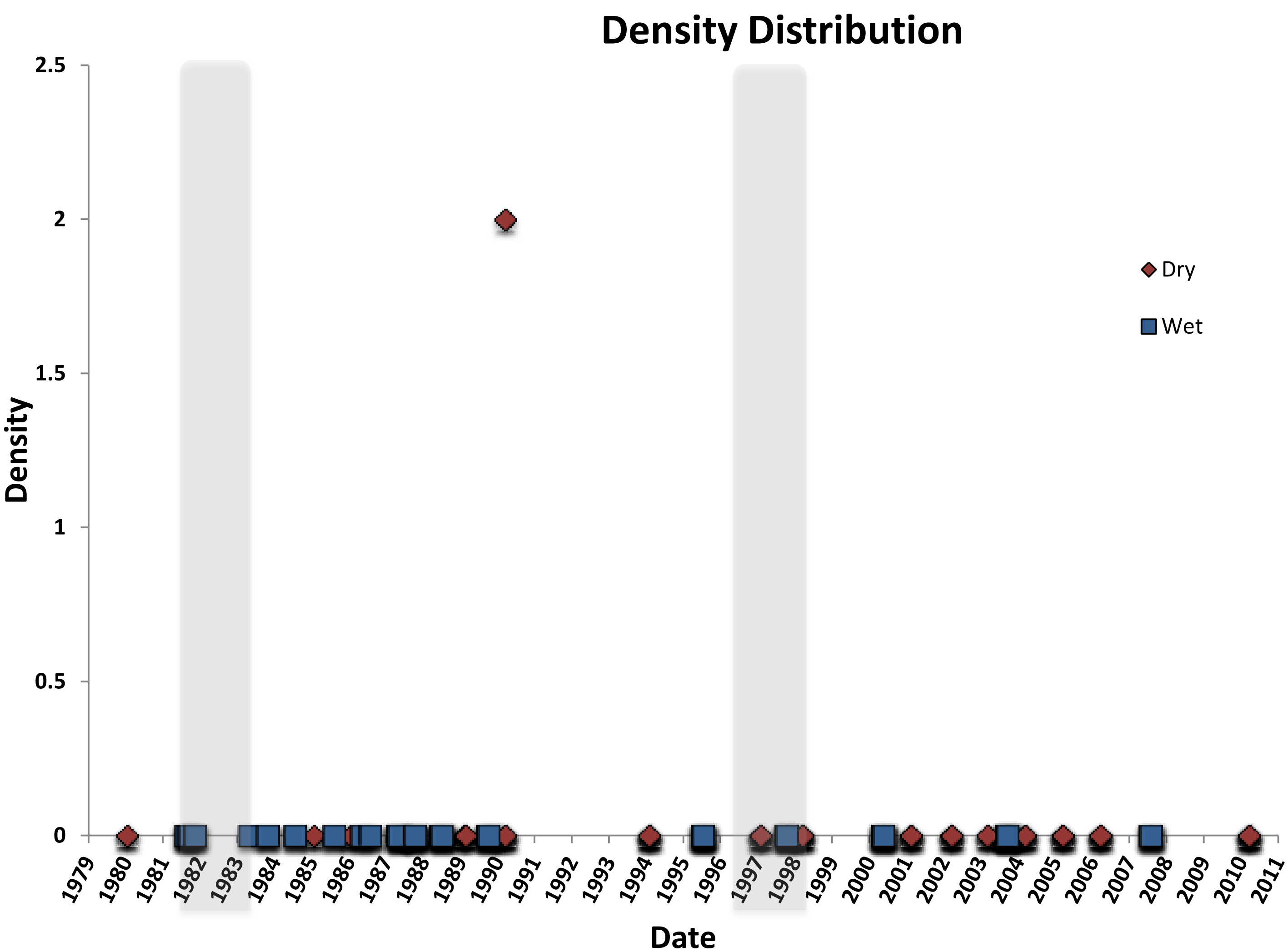
Scrawled filefish

Max. size: 110

Trophic group: Omnivore





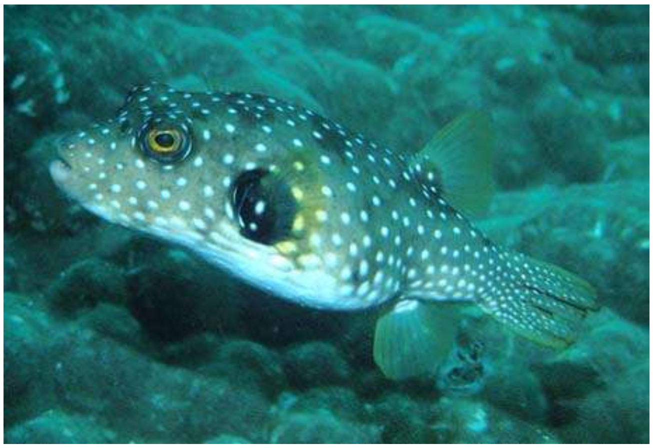


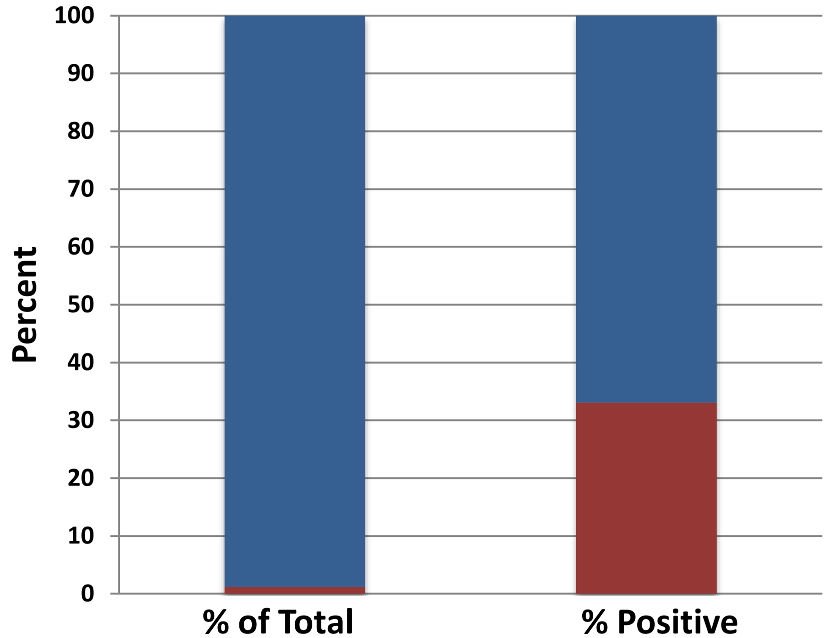
Arothron hispidus

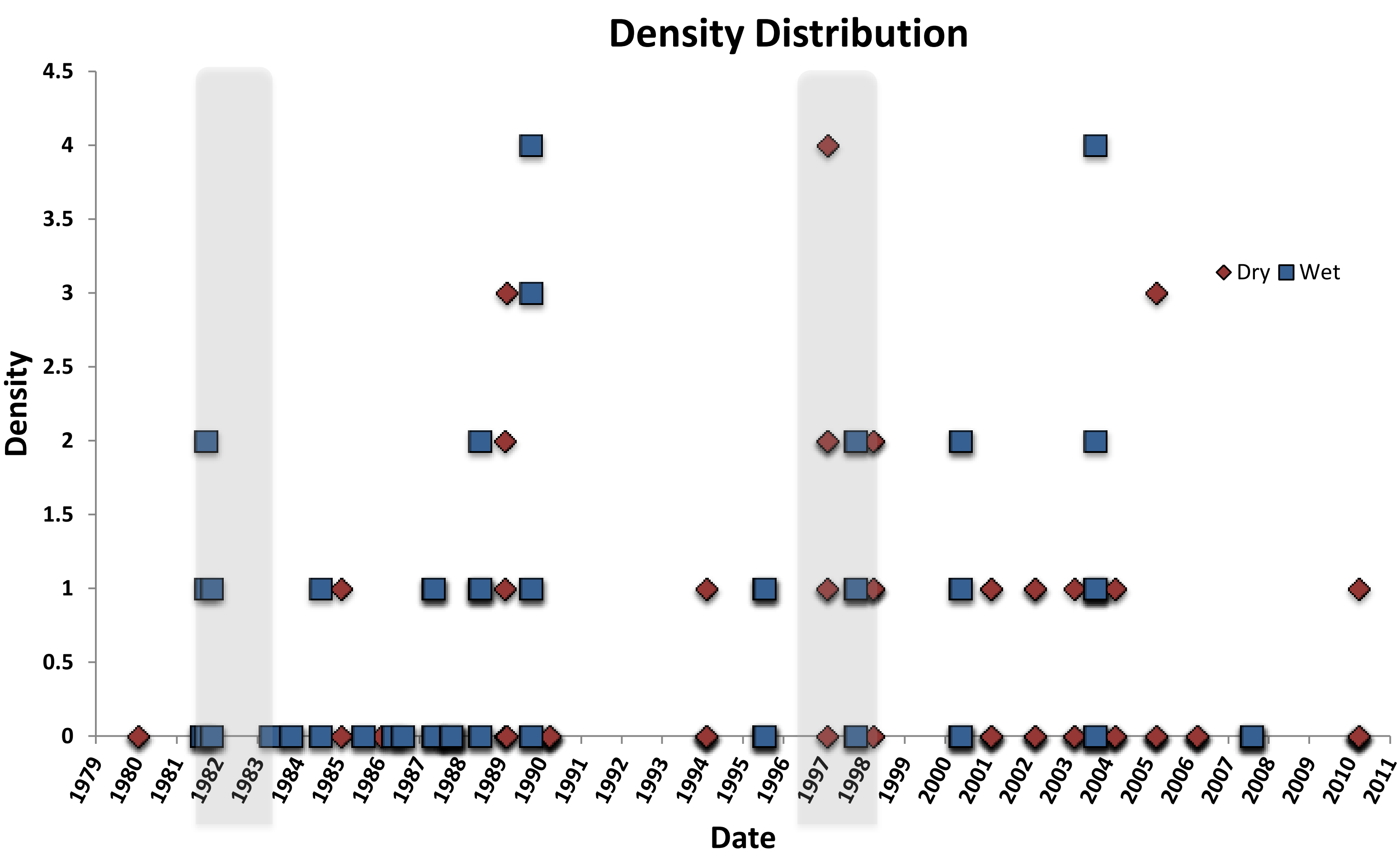
White-spotted puffer

Max. size: 50 cm

Trophic group: Omnivore





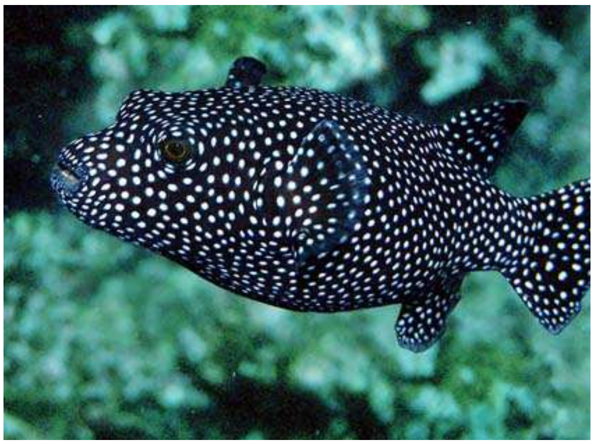


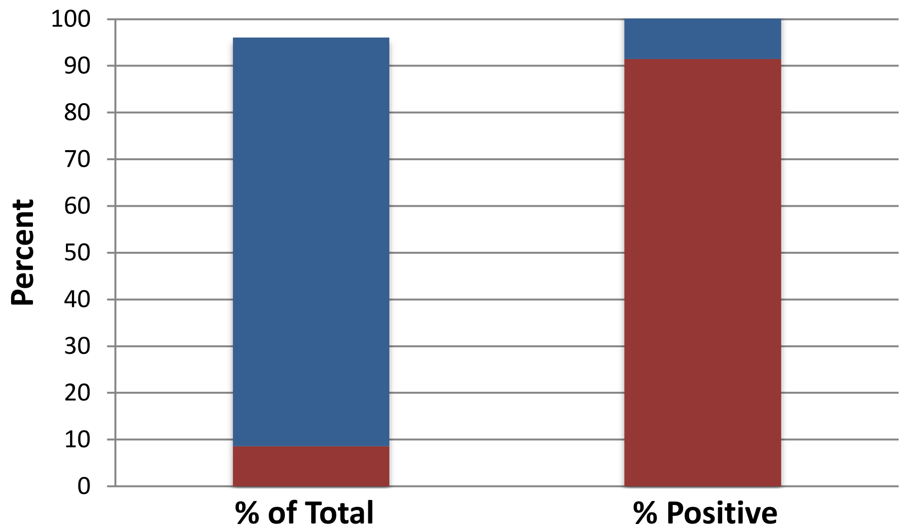
Arothron meleagris

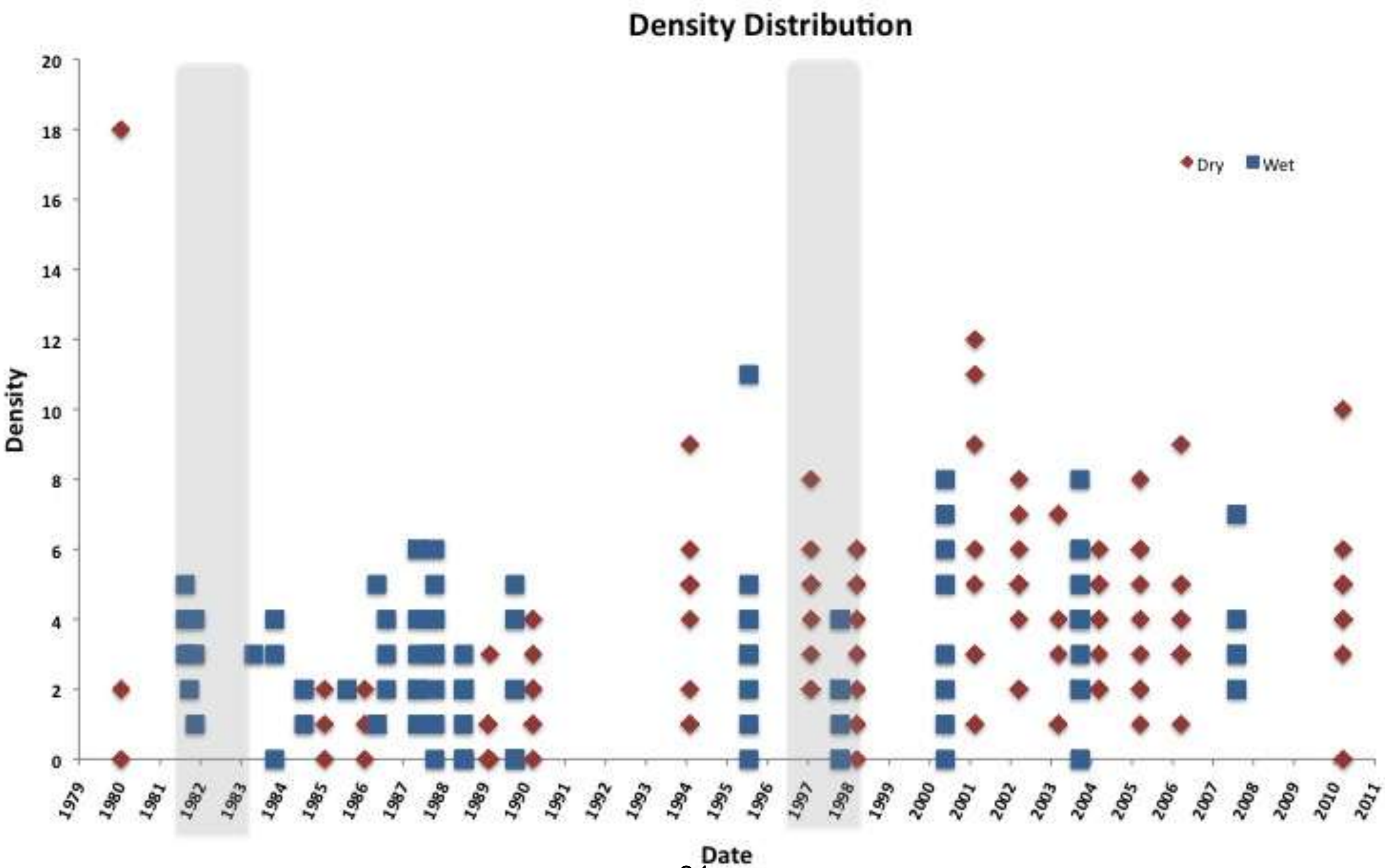
Guineafowl puffer

Max. size: 40 cm

Trophic group: Omnivore (Herbivore, Detritivore, Invertivore, Corallivore)





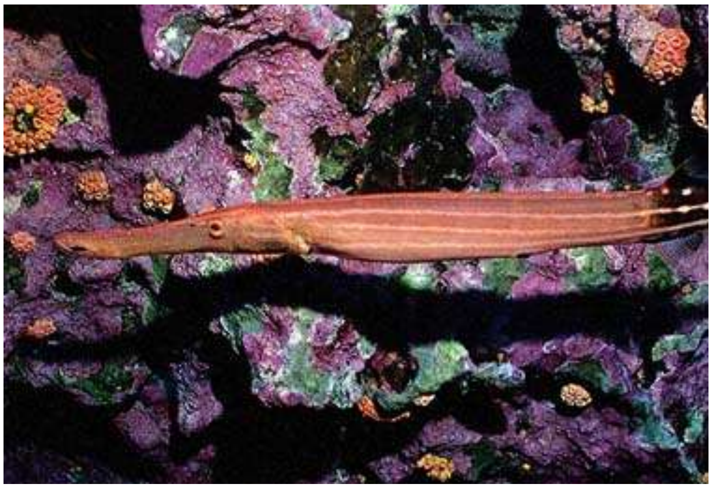


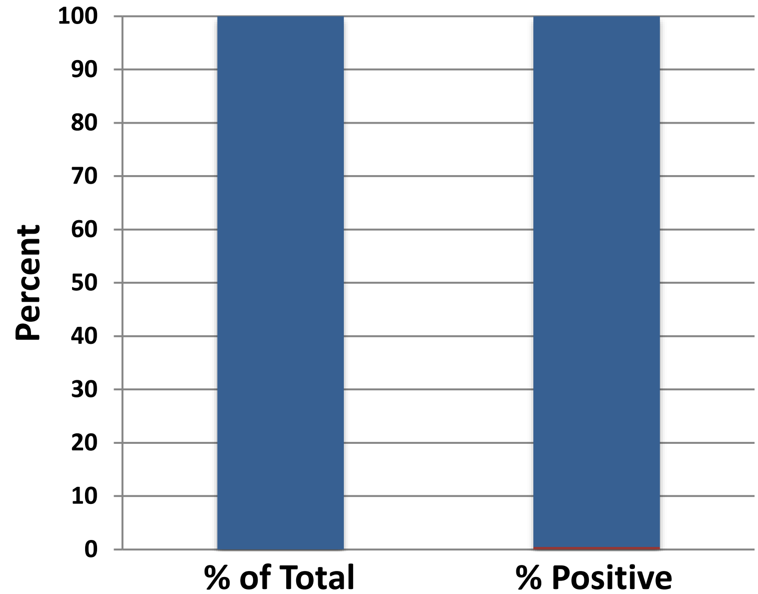
Aulostomus chinensis

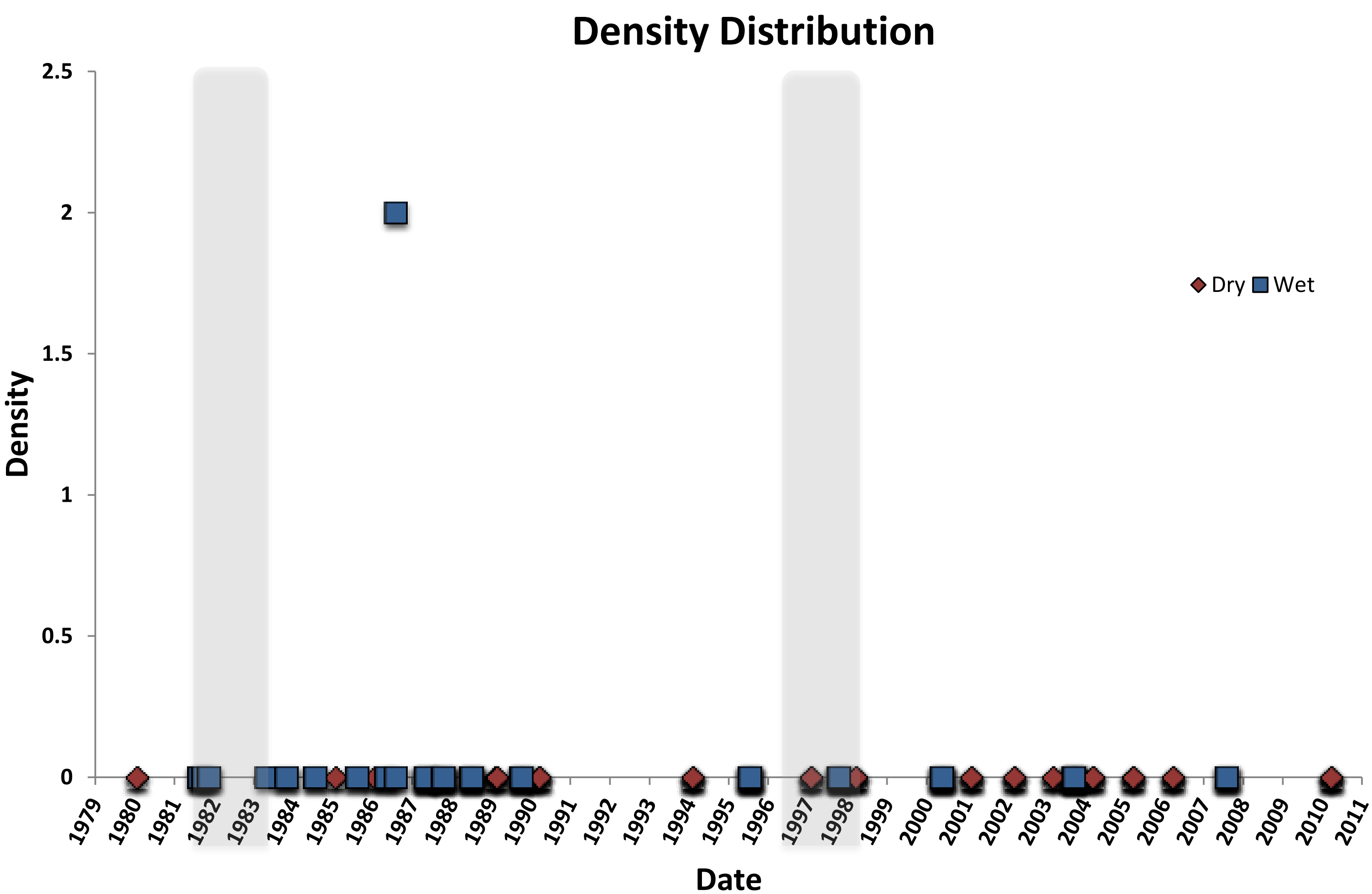
Chinese trumpetfish

Max. size: 80 cm

Trophic group: Carnivore





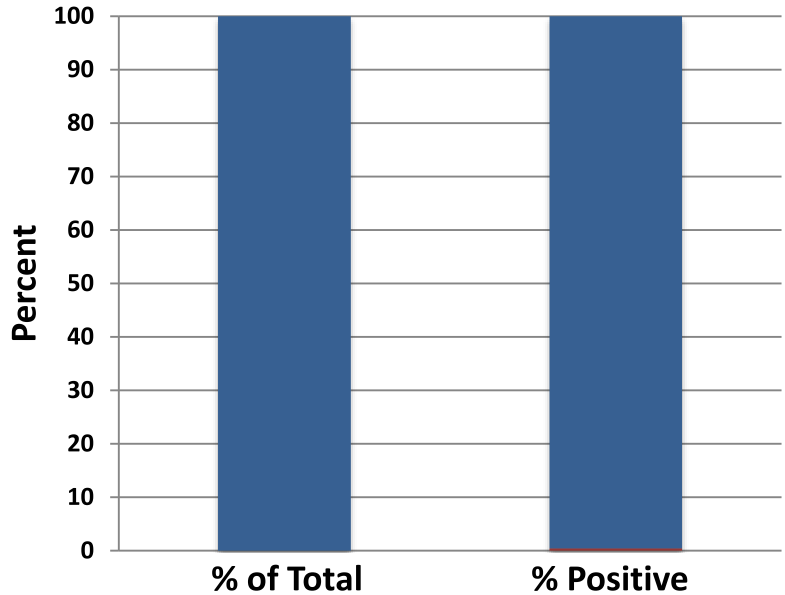


Balistes polylepis

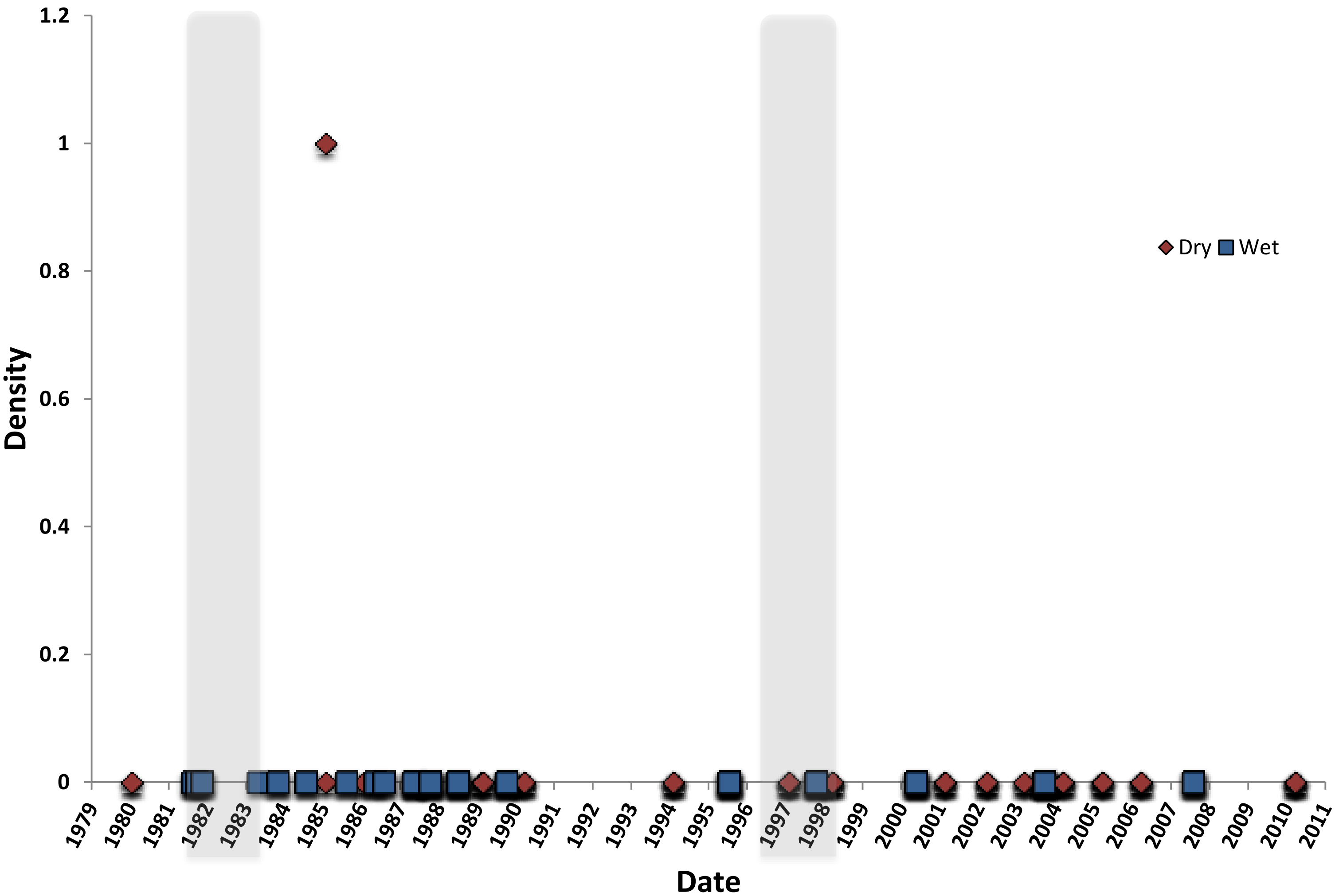
Fine-scale triggerfish

Max. size: 80 cm

Trophic group: Carnivore



Density Distribution

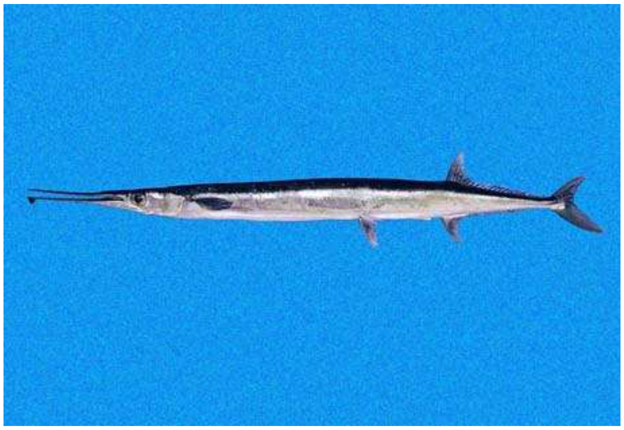


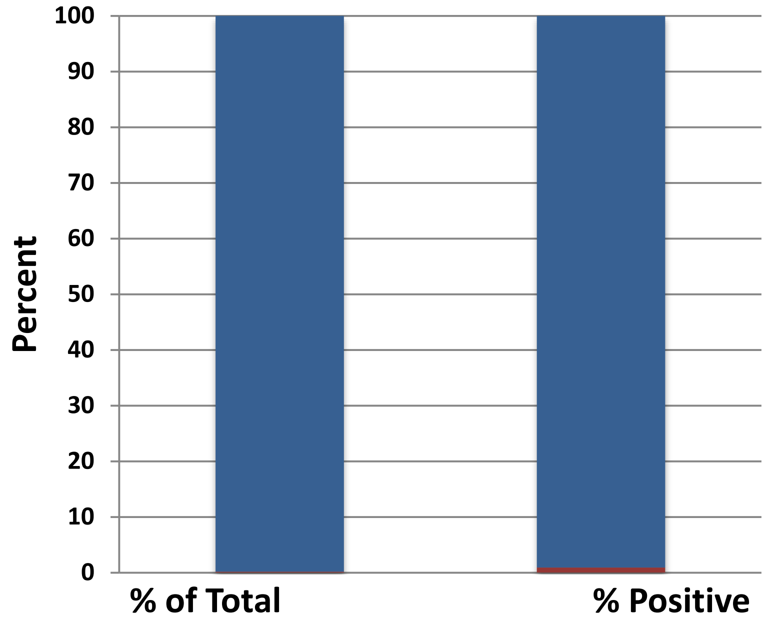
Belonidae sp.

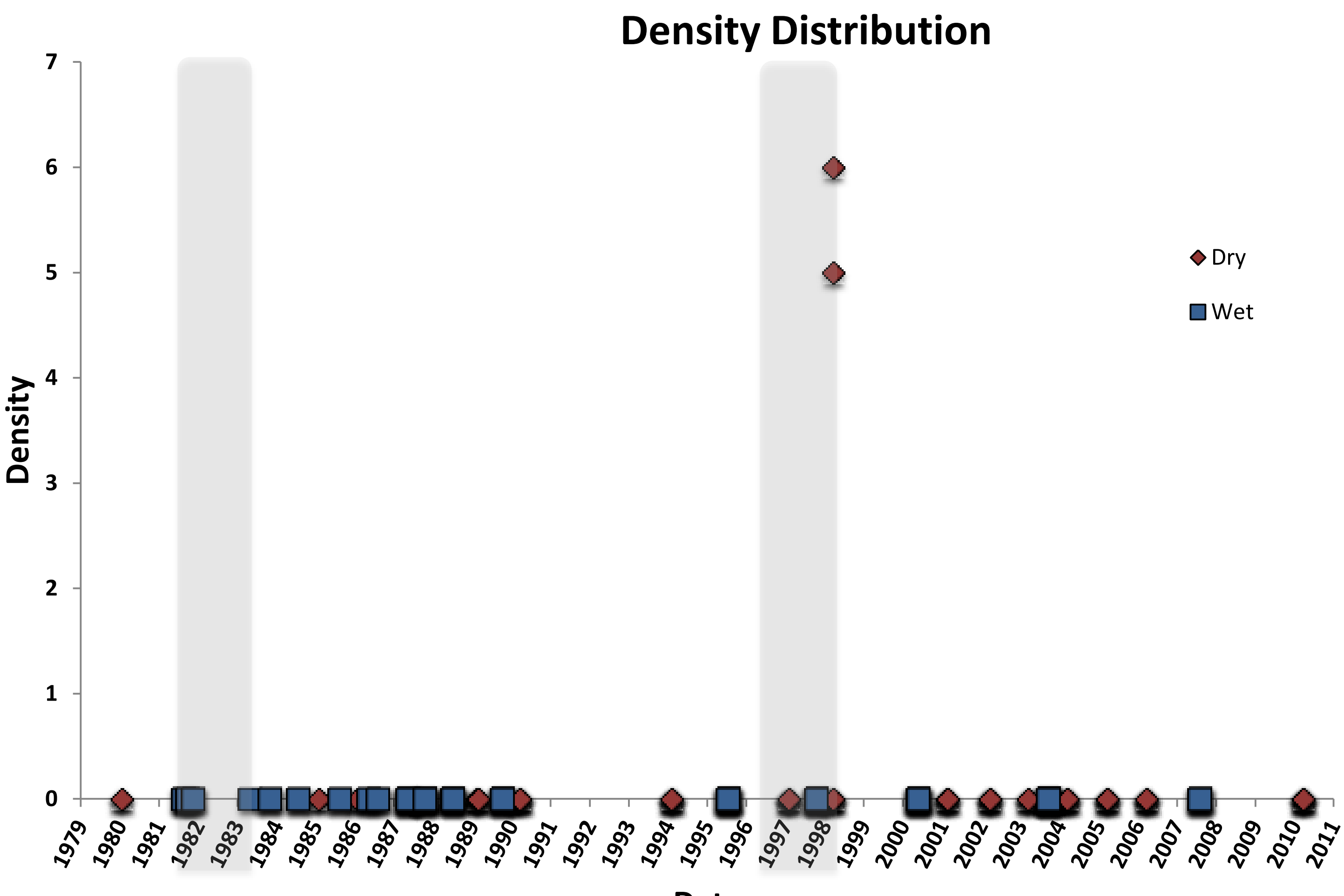
Needlefish

Max. size:

Trophic group: Carnivore





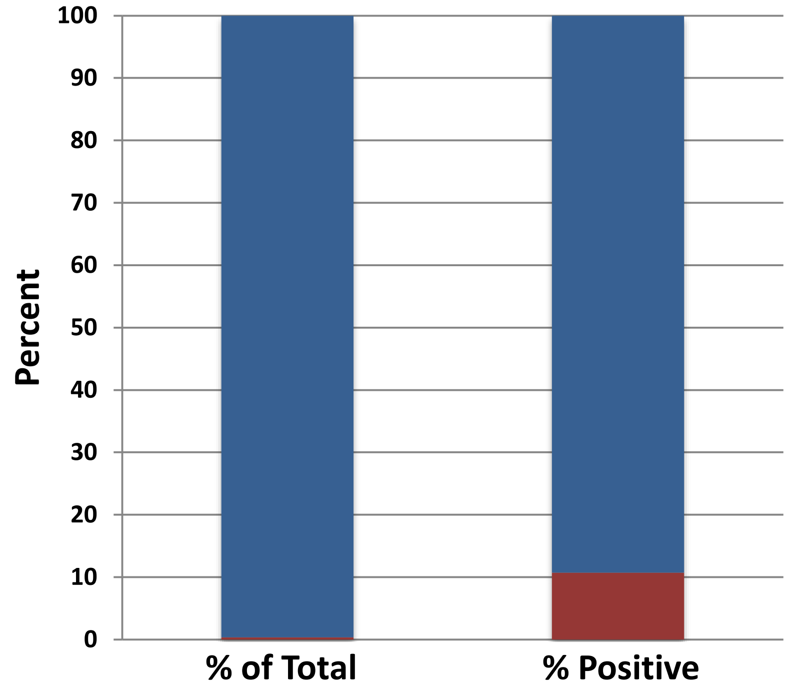


Bodianus diplotaenia

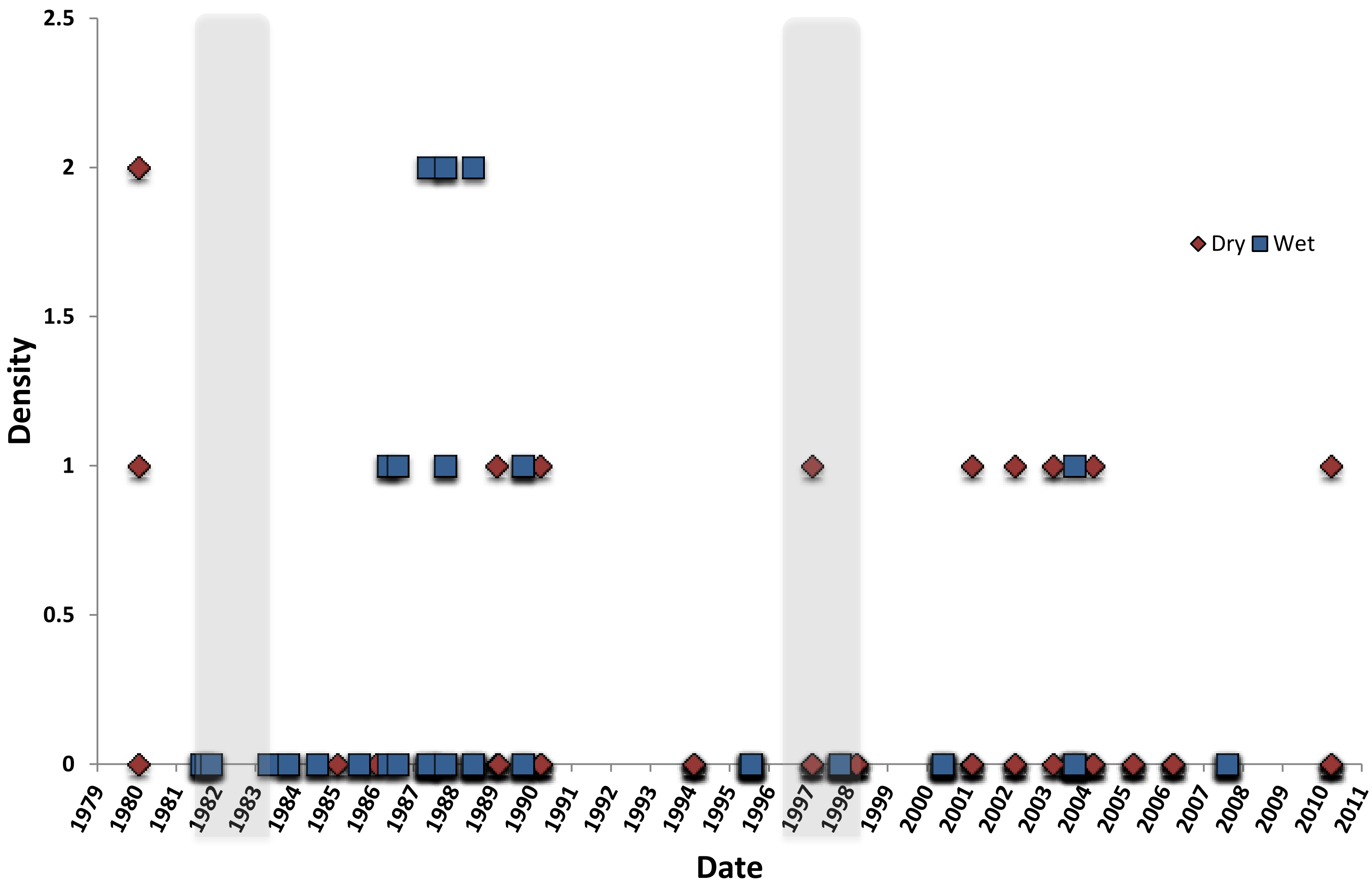
Mexican hogfish

Max. size: 76 cm

Trophic group: Invertivore



Density Distribution

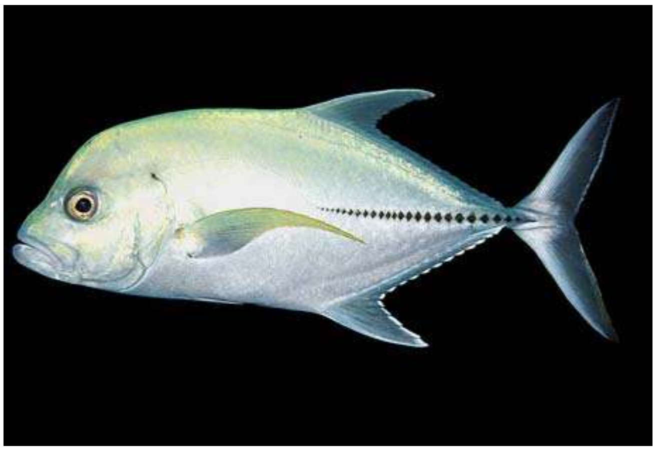


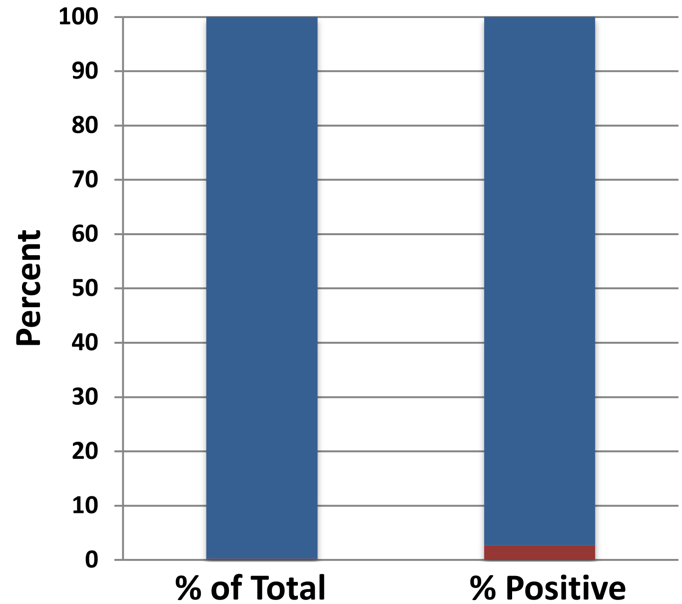
Carangidae spp.

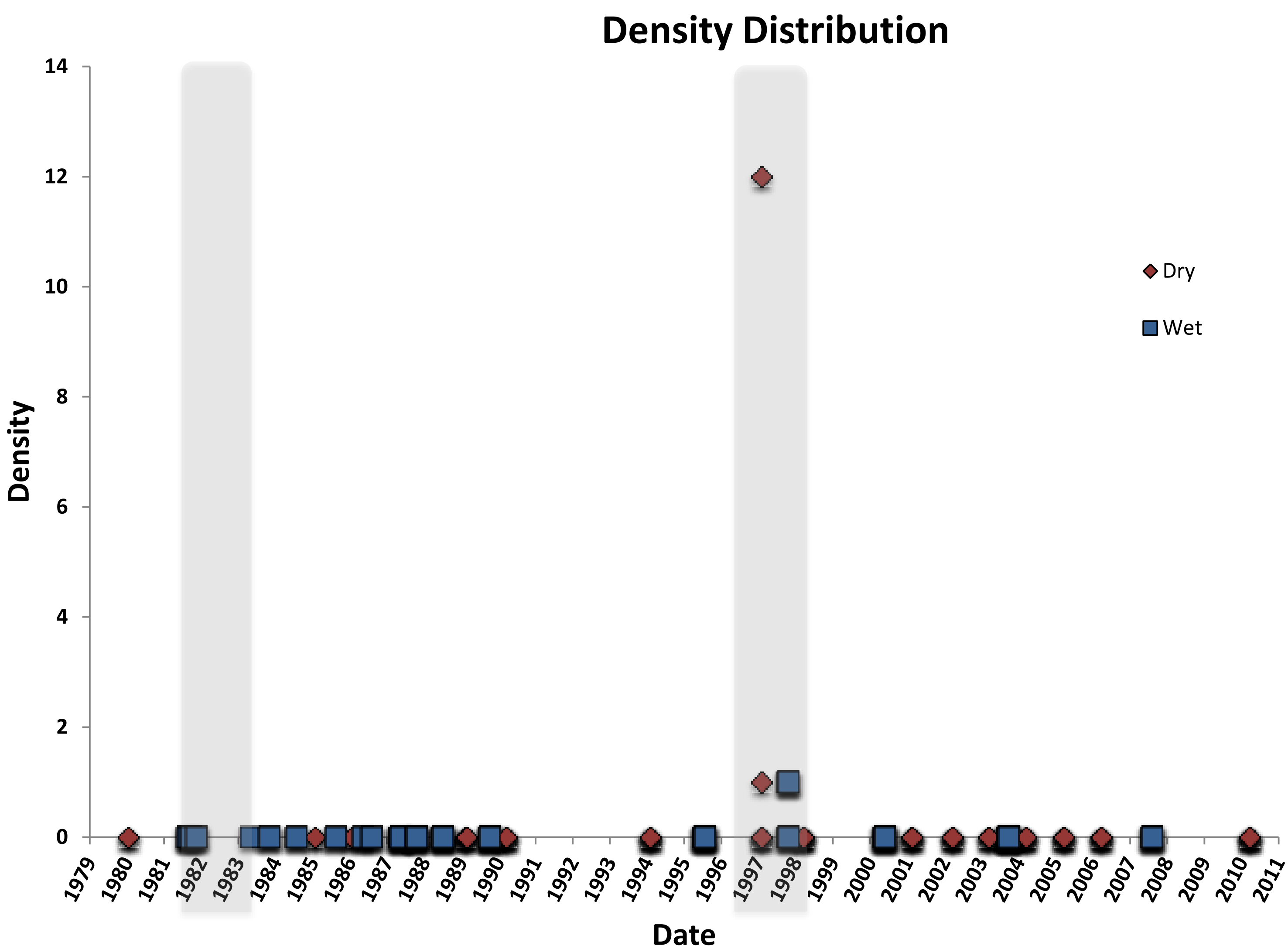
Jacks

Max. size: N/A

Trophic group: Carnivore





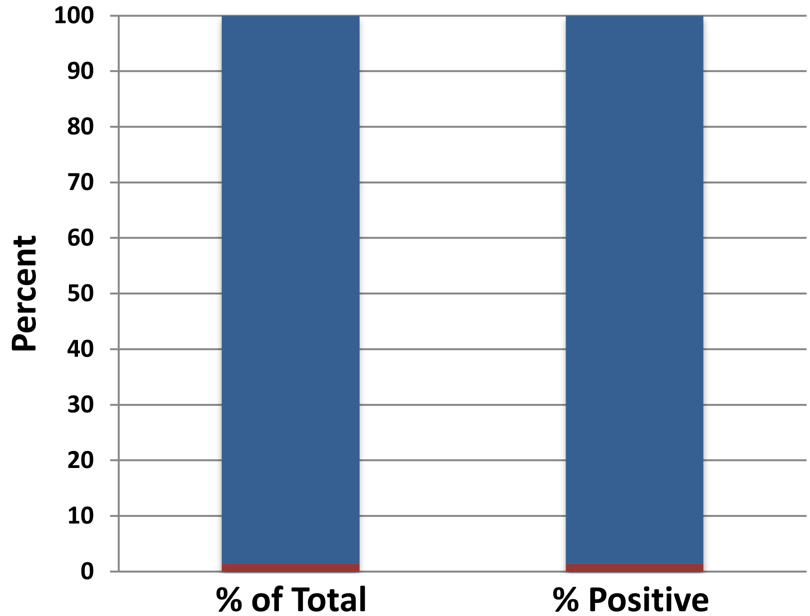


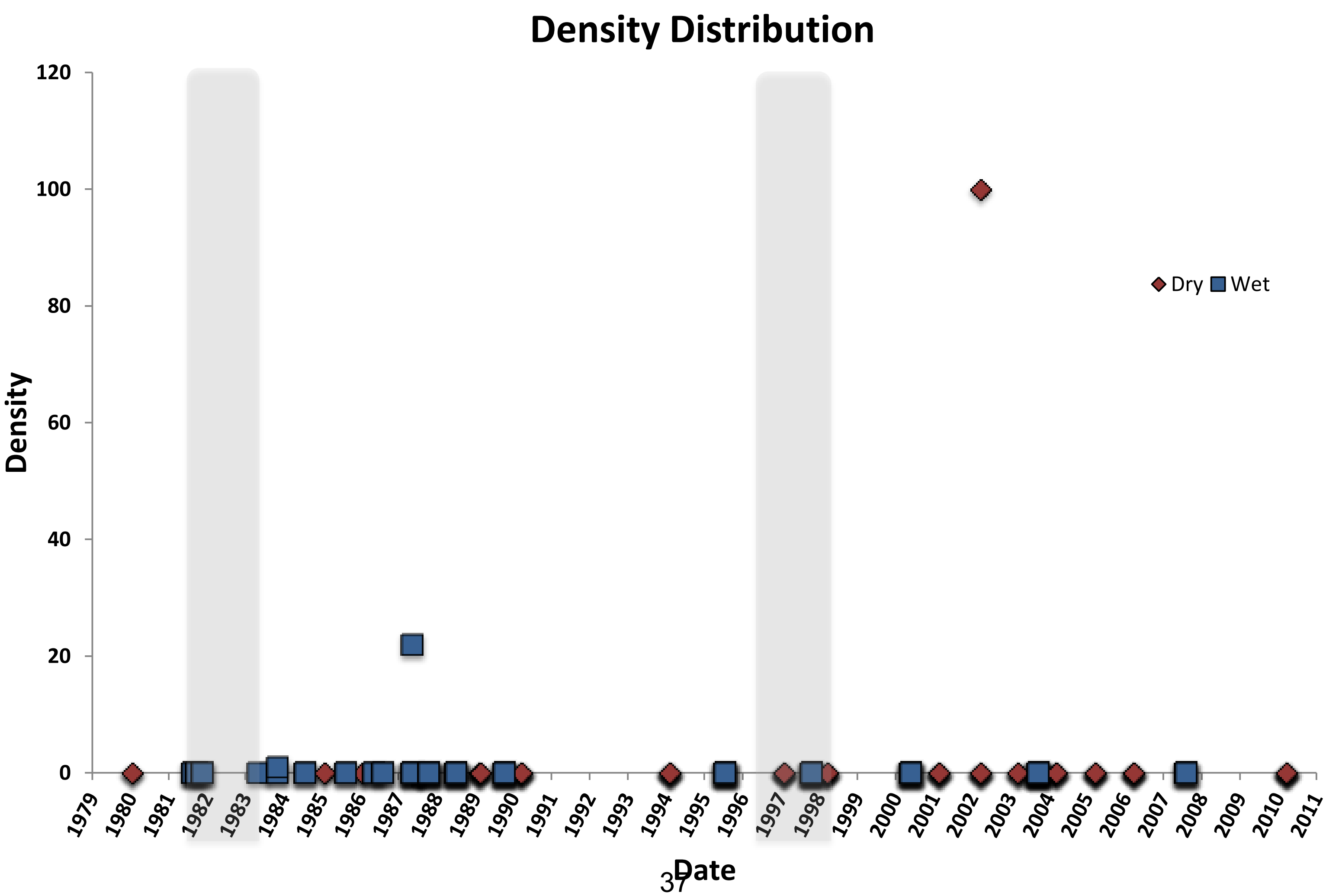
Caranx caballus

Green jack

Max. size: at least 70 cm

Trophic group: Carnivore



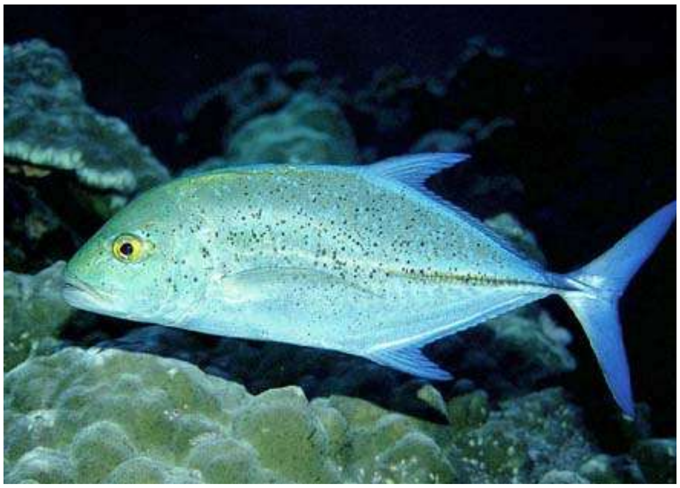


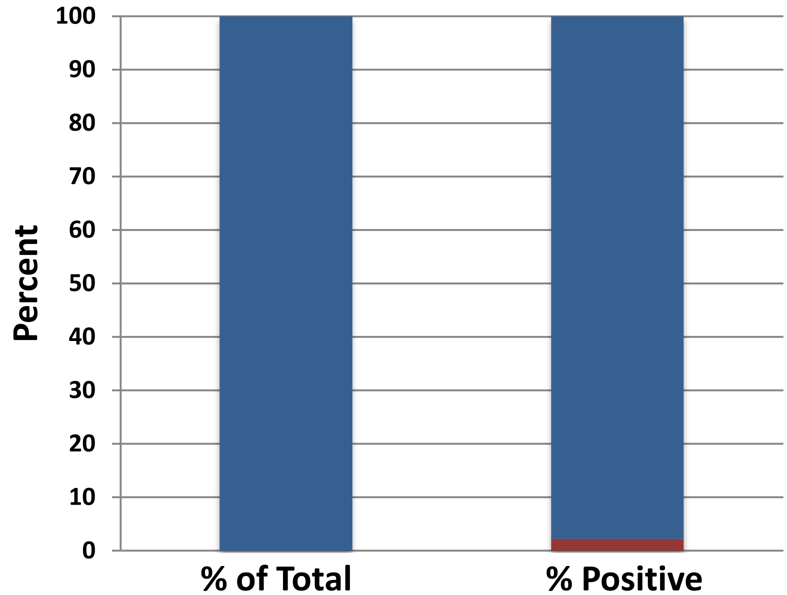
Caranx melampygus

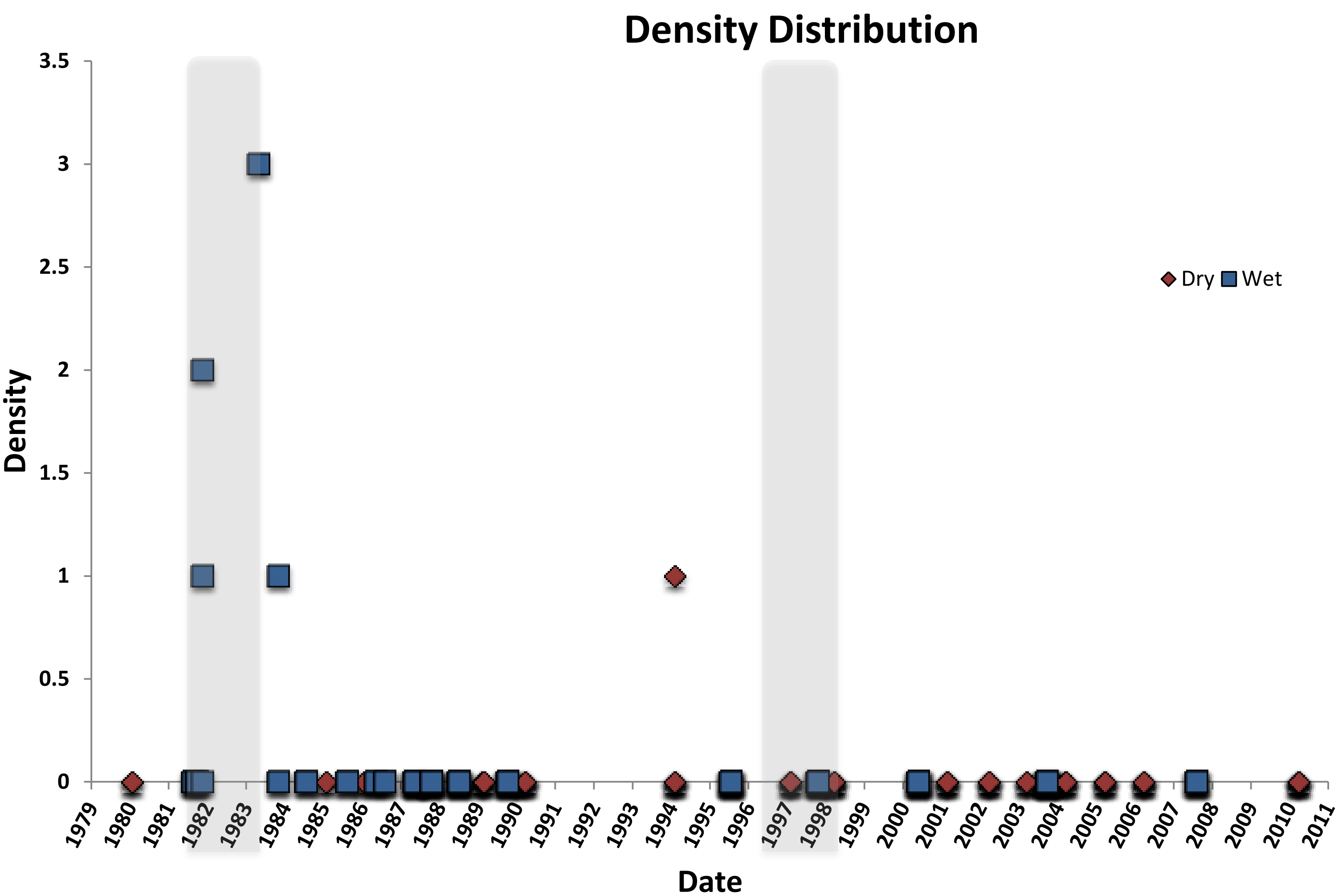
Bluefin trevally

Max. size: 100 cm

Trophic group: Carnivore





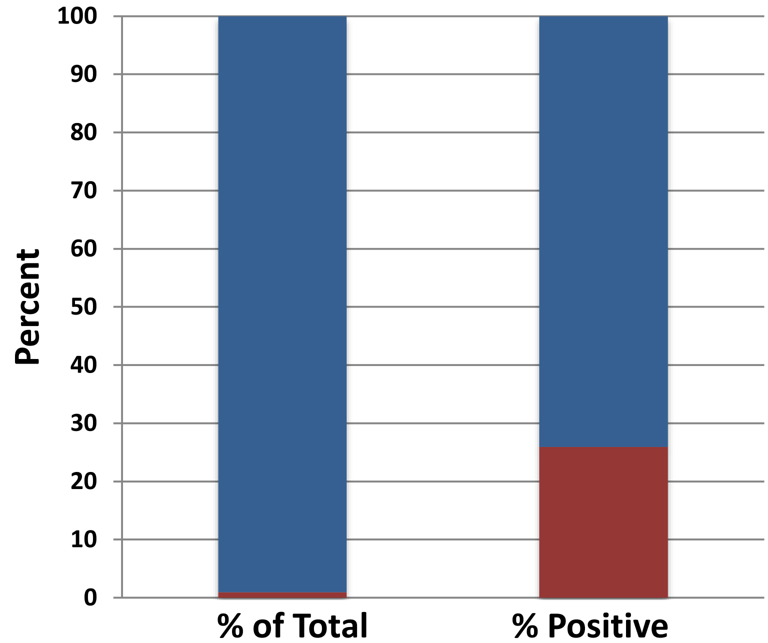


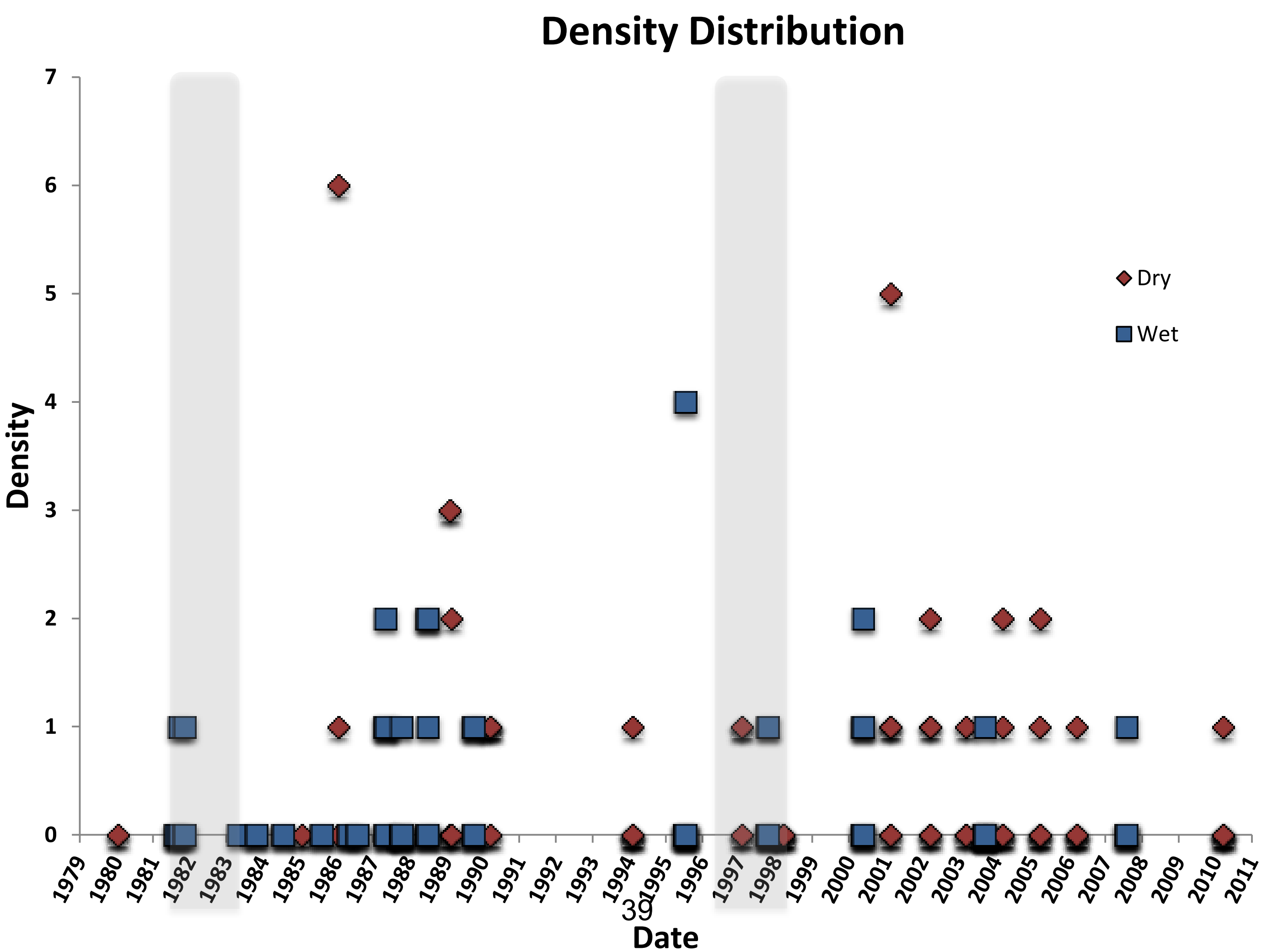
Cephalopholis panamensis

Panamic graysby

Max. size: 30.5 cm

Trophic group: Carnivore



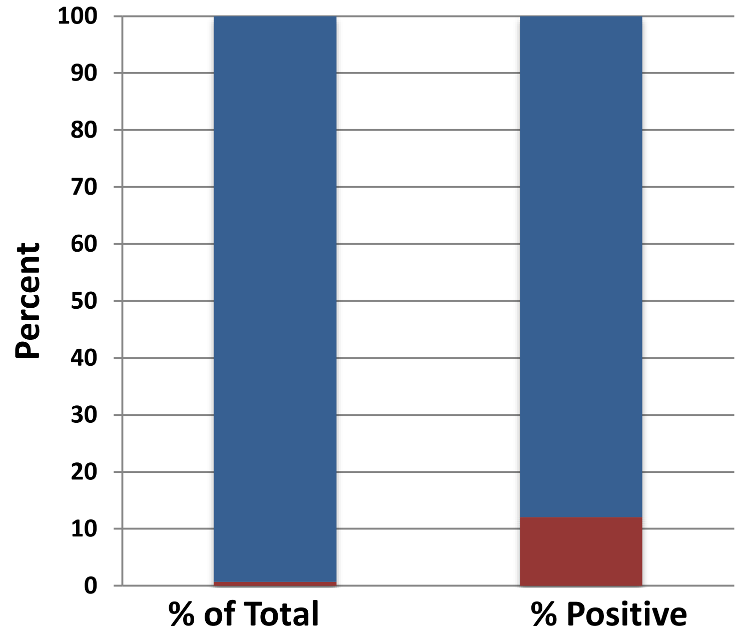


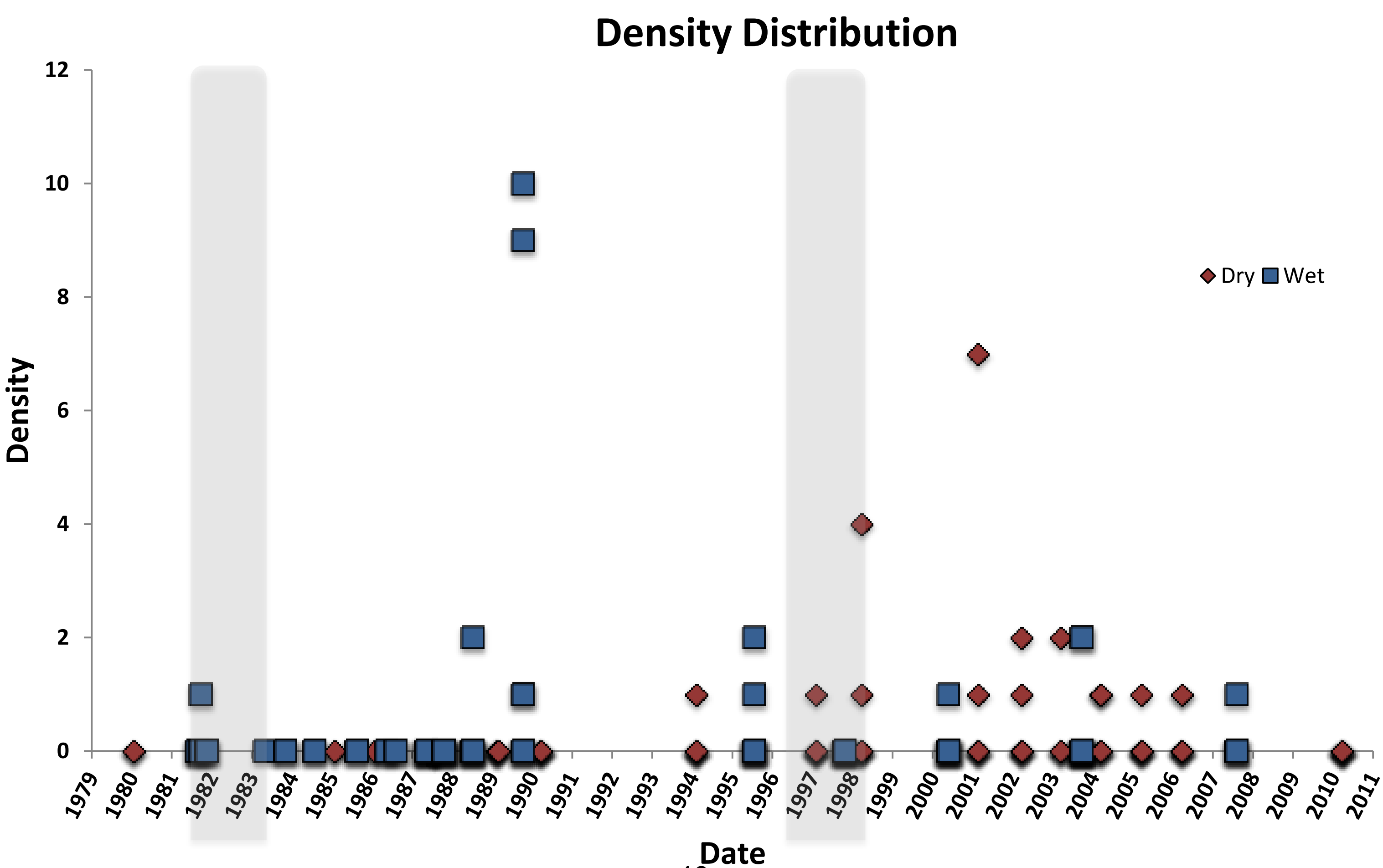
Chaetodon humeralis

Threebanded butterflyfish

Max. size: 26.4 cm

Trophic group: Omnivore (Herbivore, Invertivore, Corallivore)



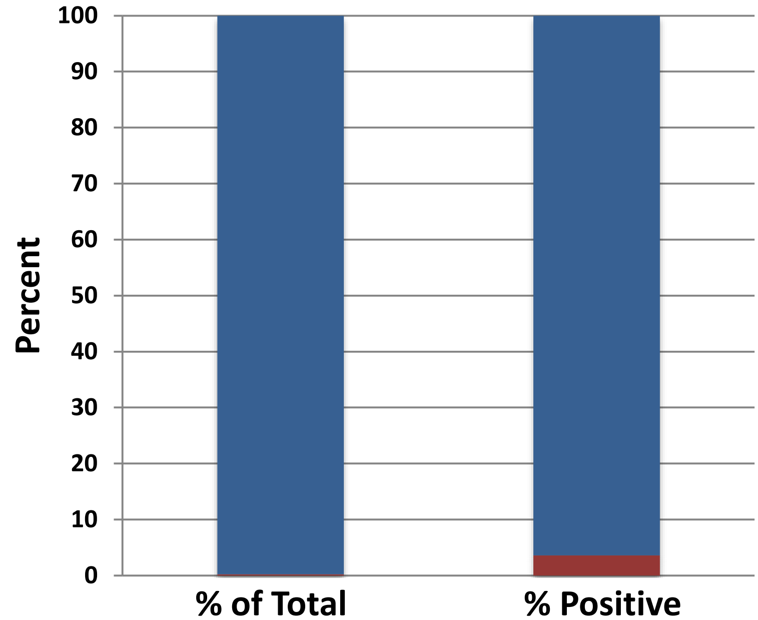


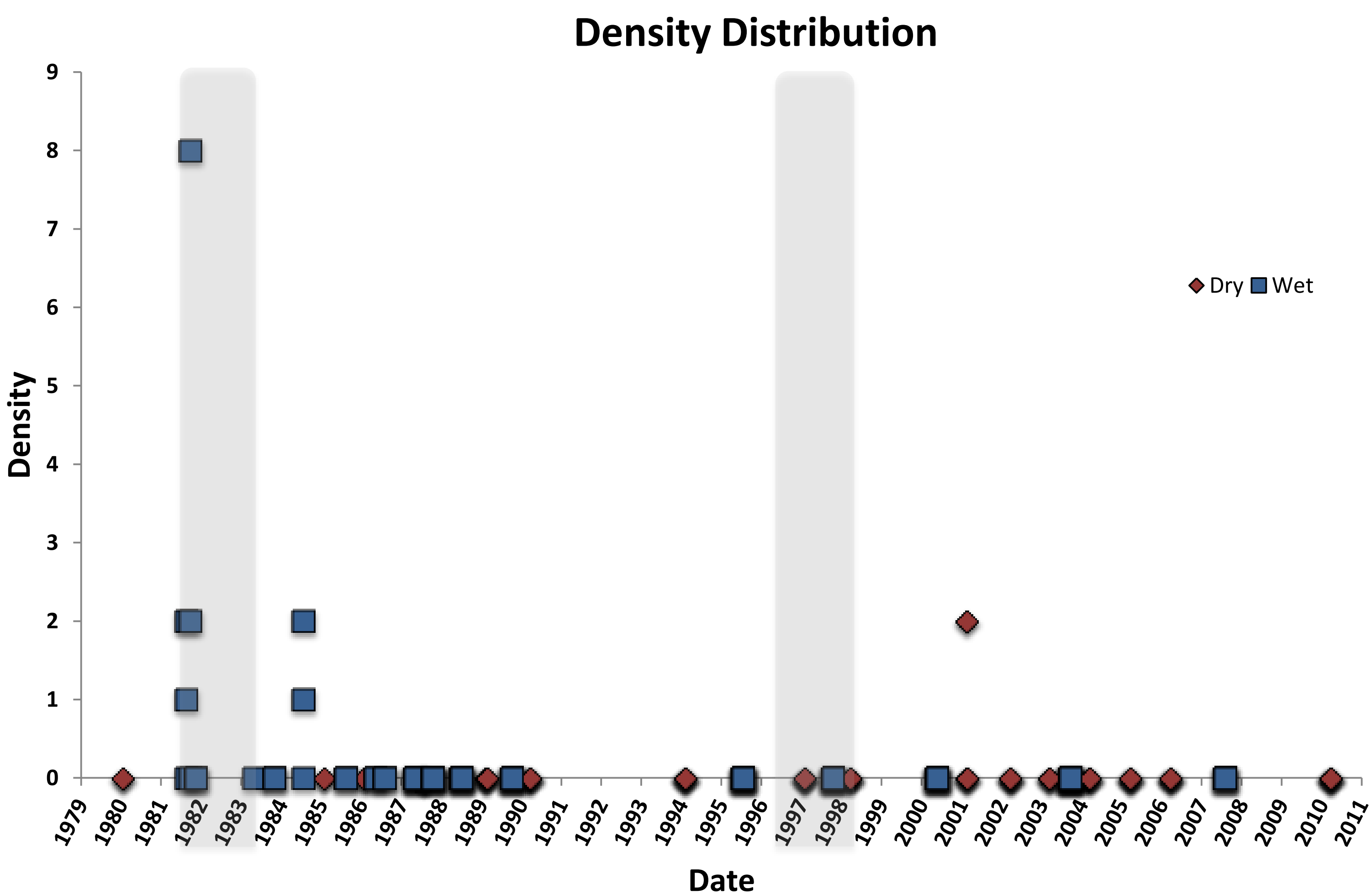
Ctenochaetus marginatus

Blue-spotted surgeonfish

Max. size: 30 cm

Trophic group: Herbivore



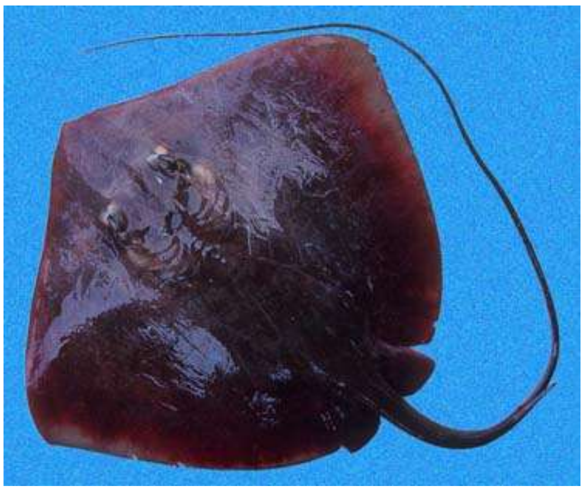


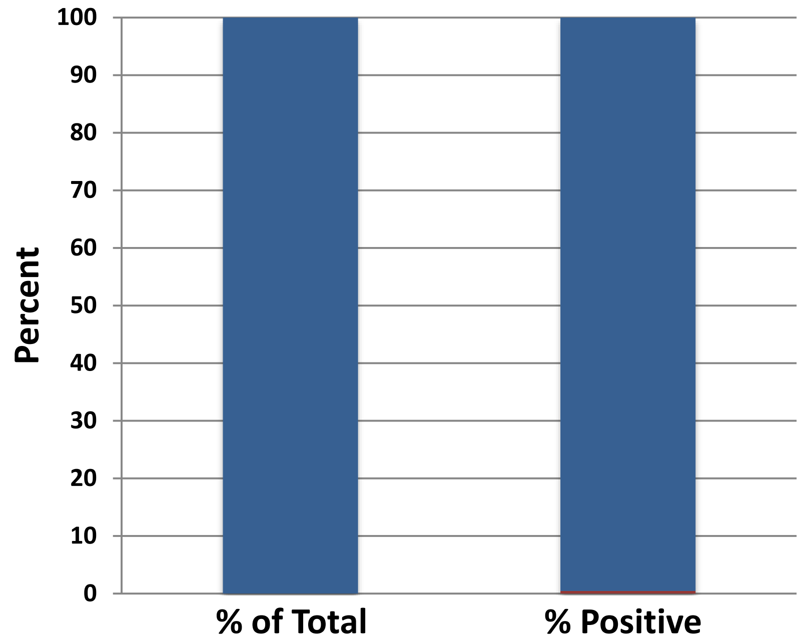
Dasyatis longus

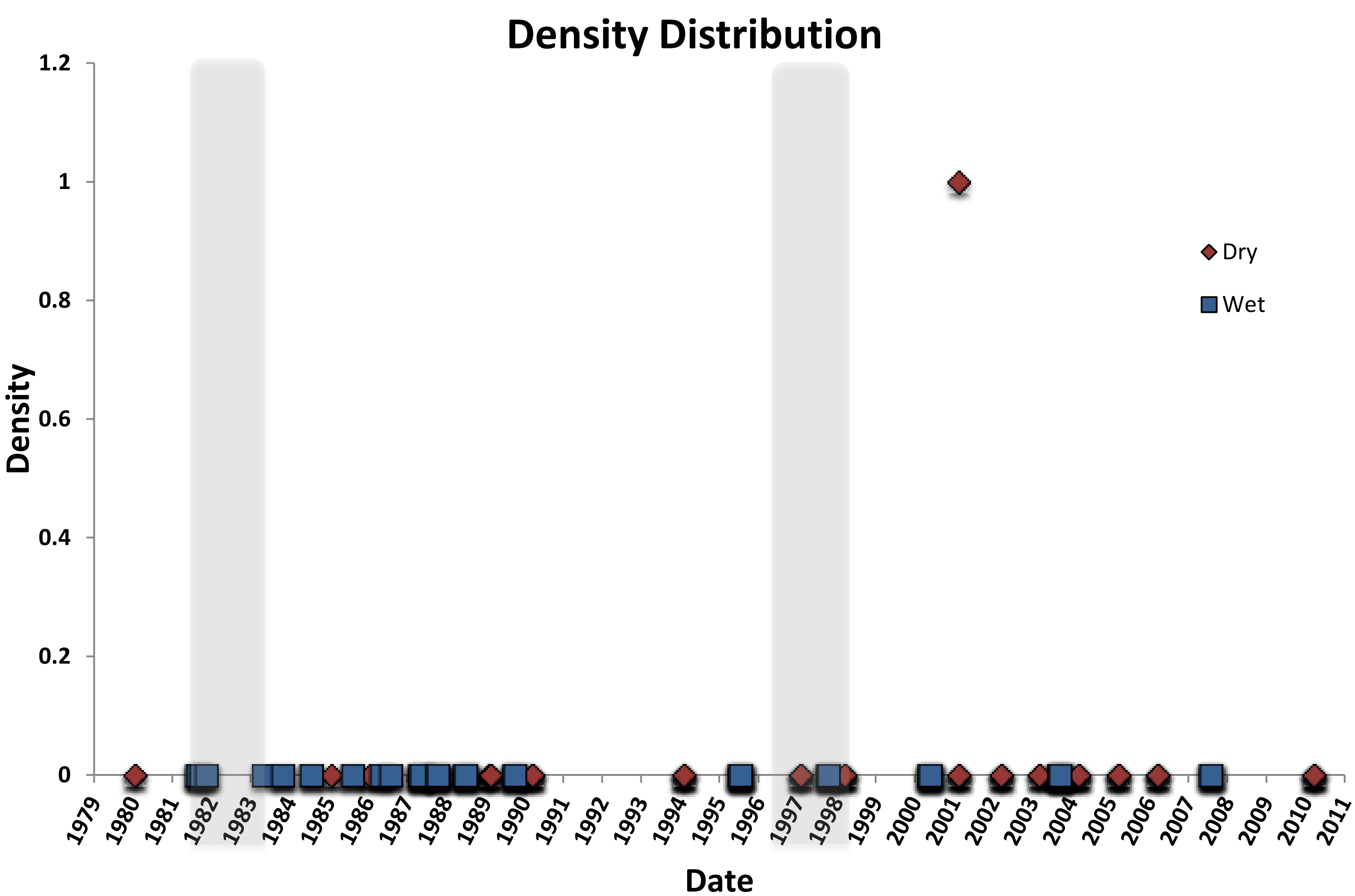
Longtail stingray

Max. size: Tail Length of 257 cm
Disc width of 117 cm

Trophic group: Carnivore





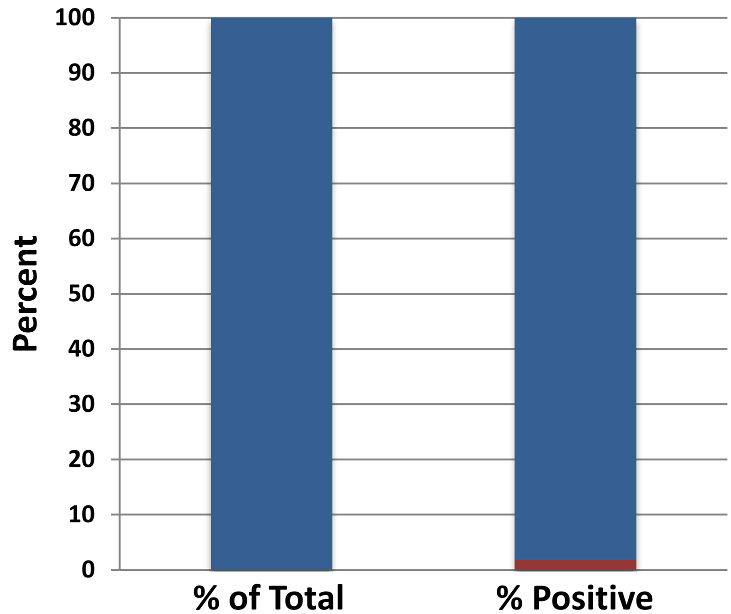


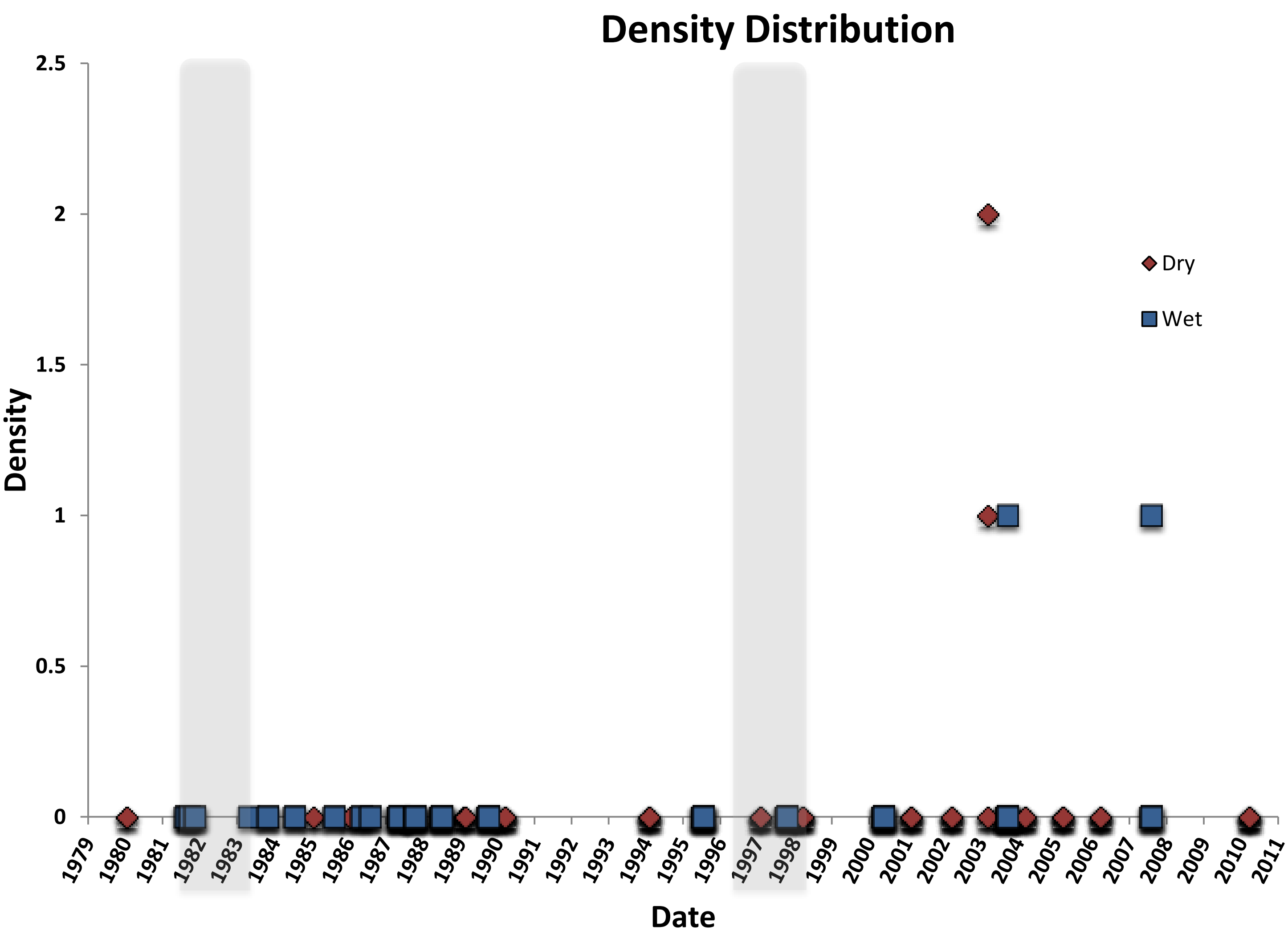
Dermatolepis dermatolepis

Leather bass

Max. size: 100 cm

Trophic group: Carnivore



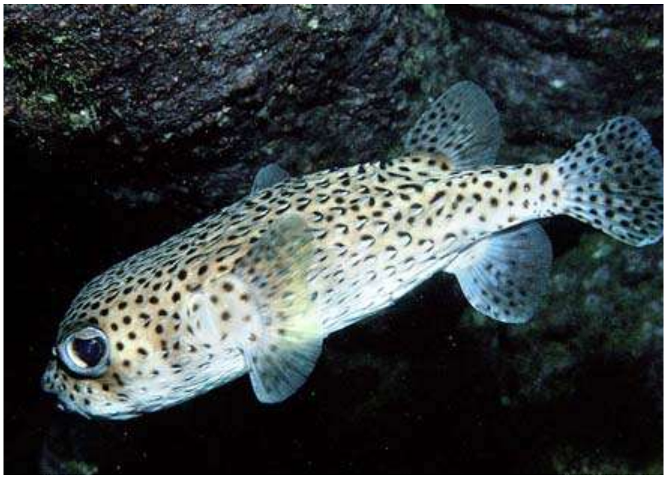


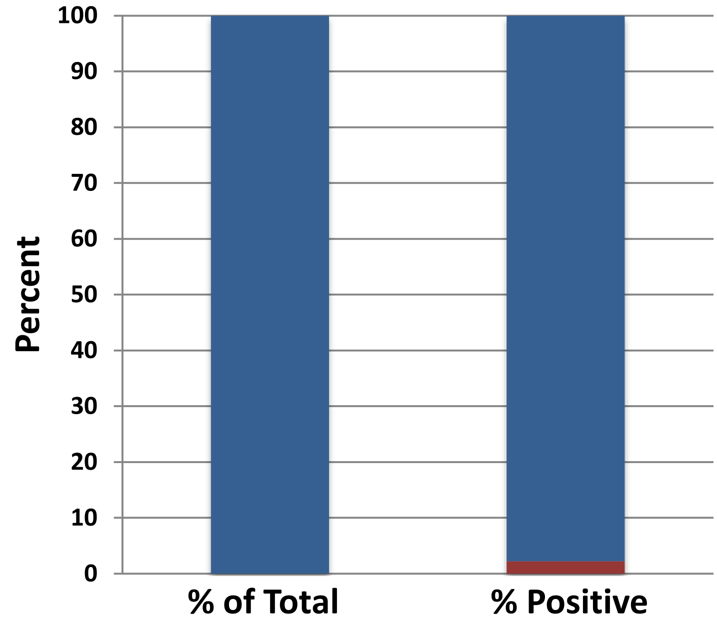
Diodon hystrix

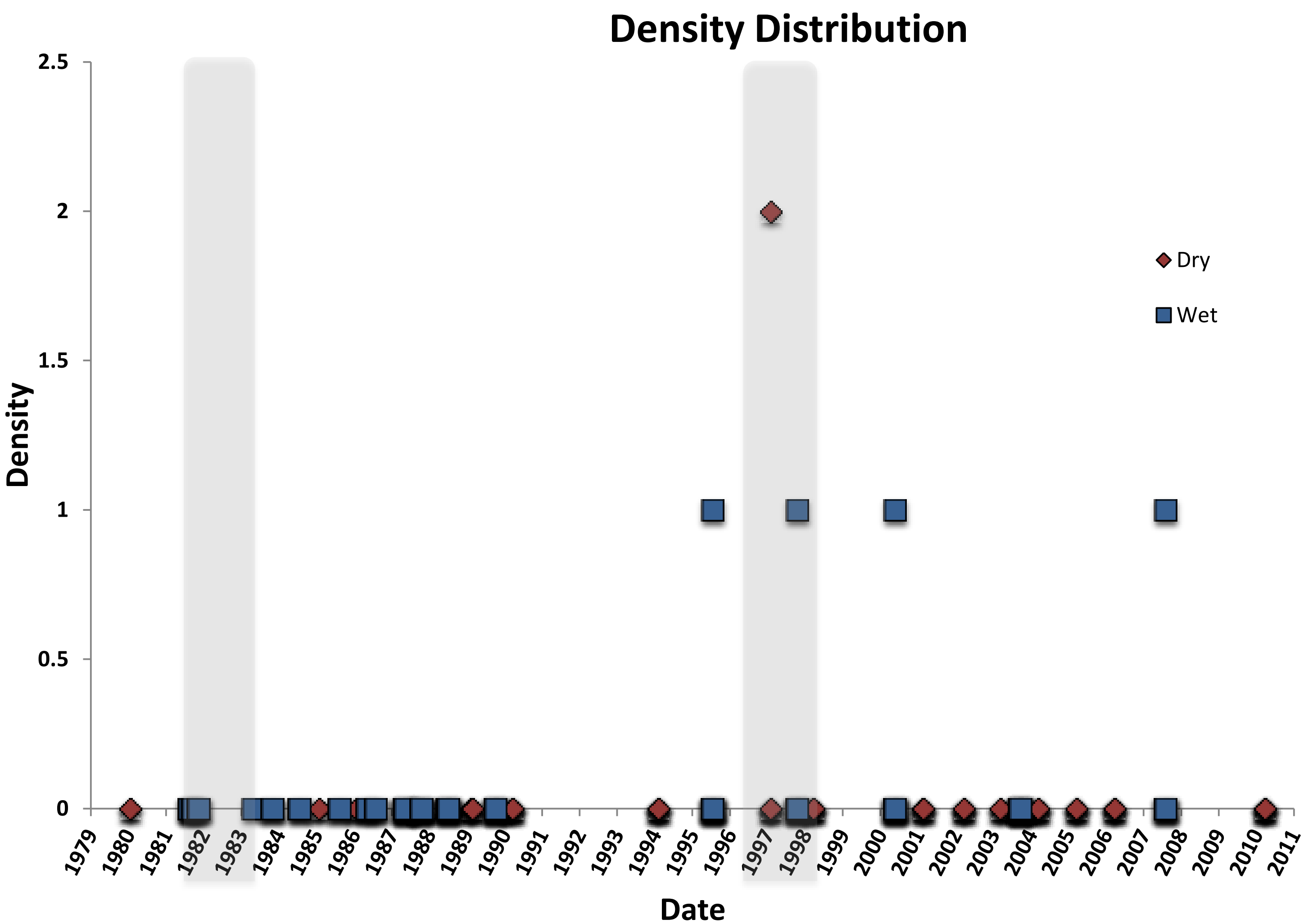
Spot-fin porcupinefish

Max. size: 91 cm

Trophic group: Invertivore





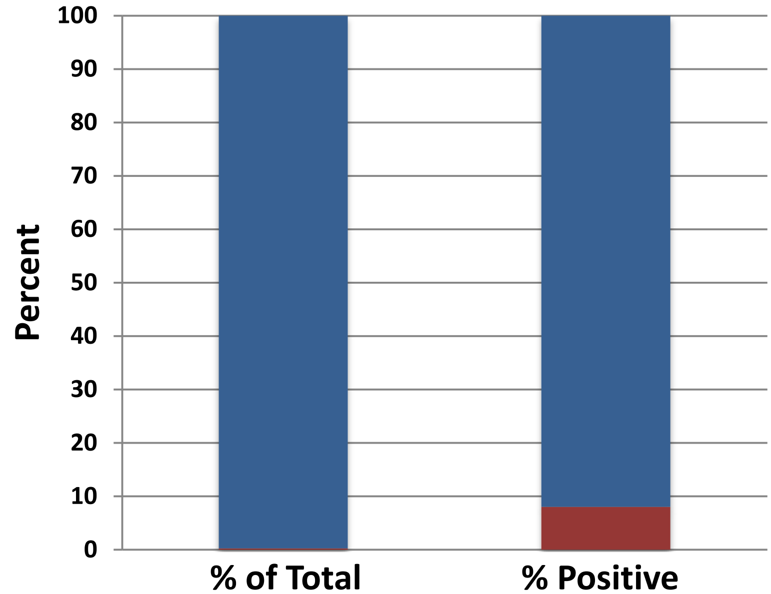


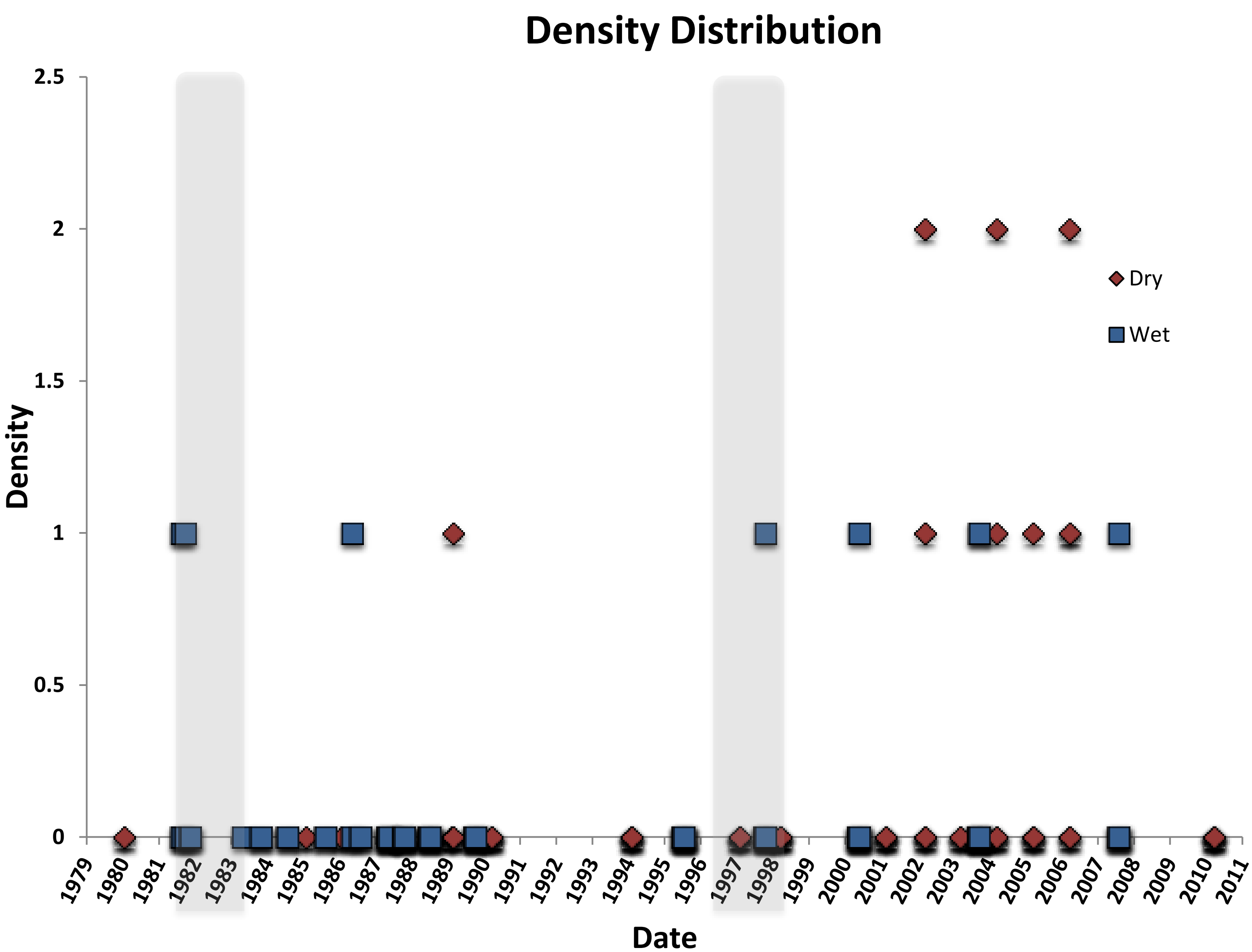
Diodon holocanthus

Freckled porcupinefish

Max. size: 50 cm

Trophic group: Invertivore



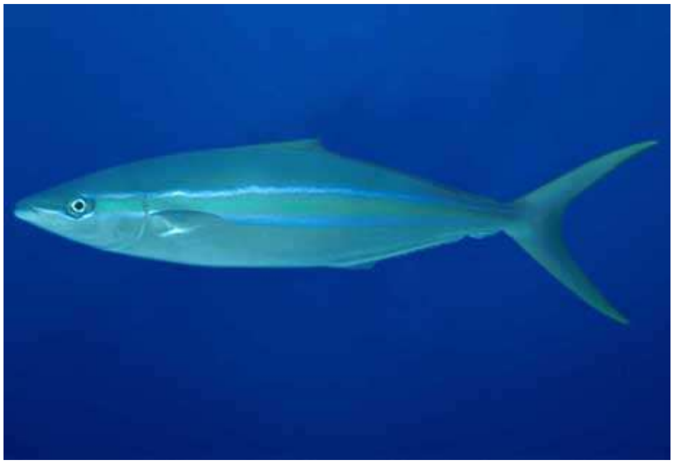


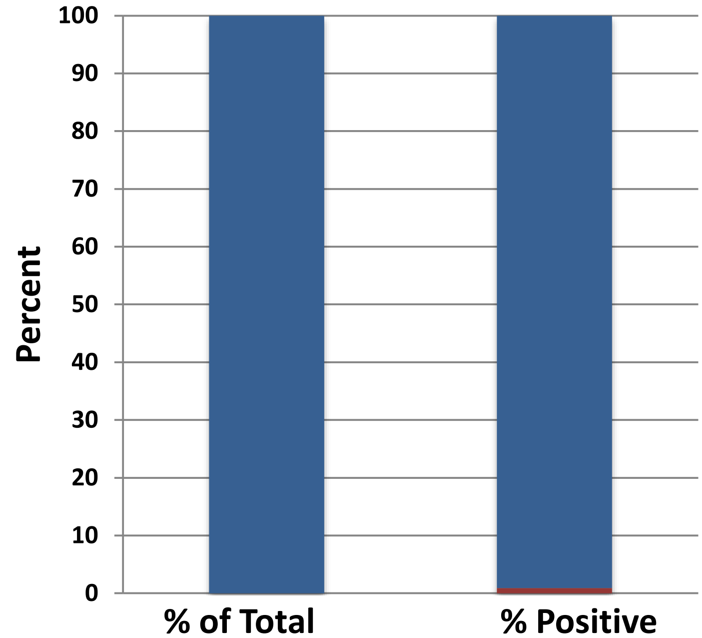
Elagatis bipinnulata

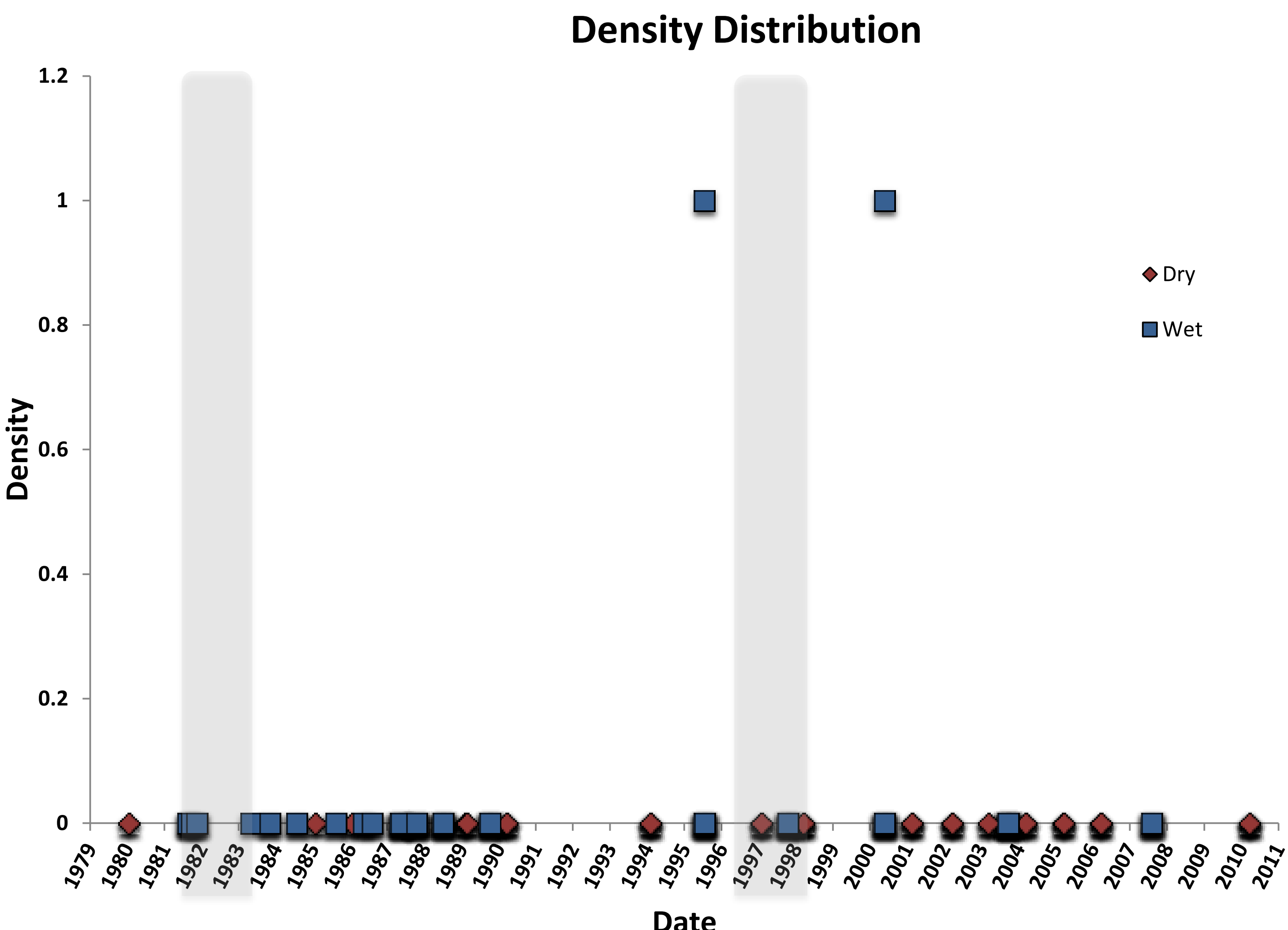
Rainbow runner

Max. size: 180 cm max (usually 80 cm)

Trophic group: Carnivore





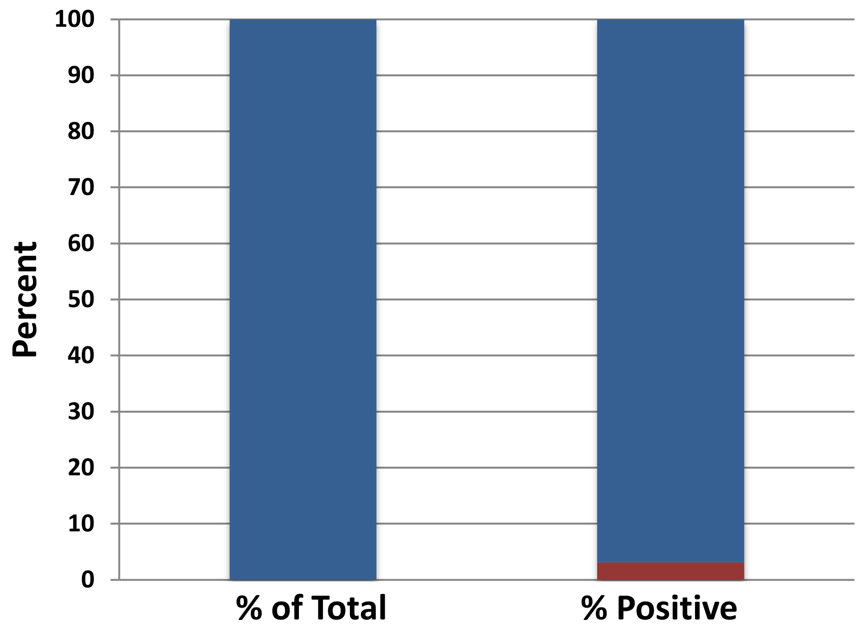


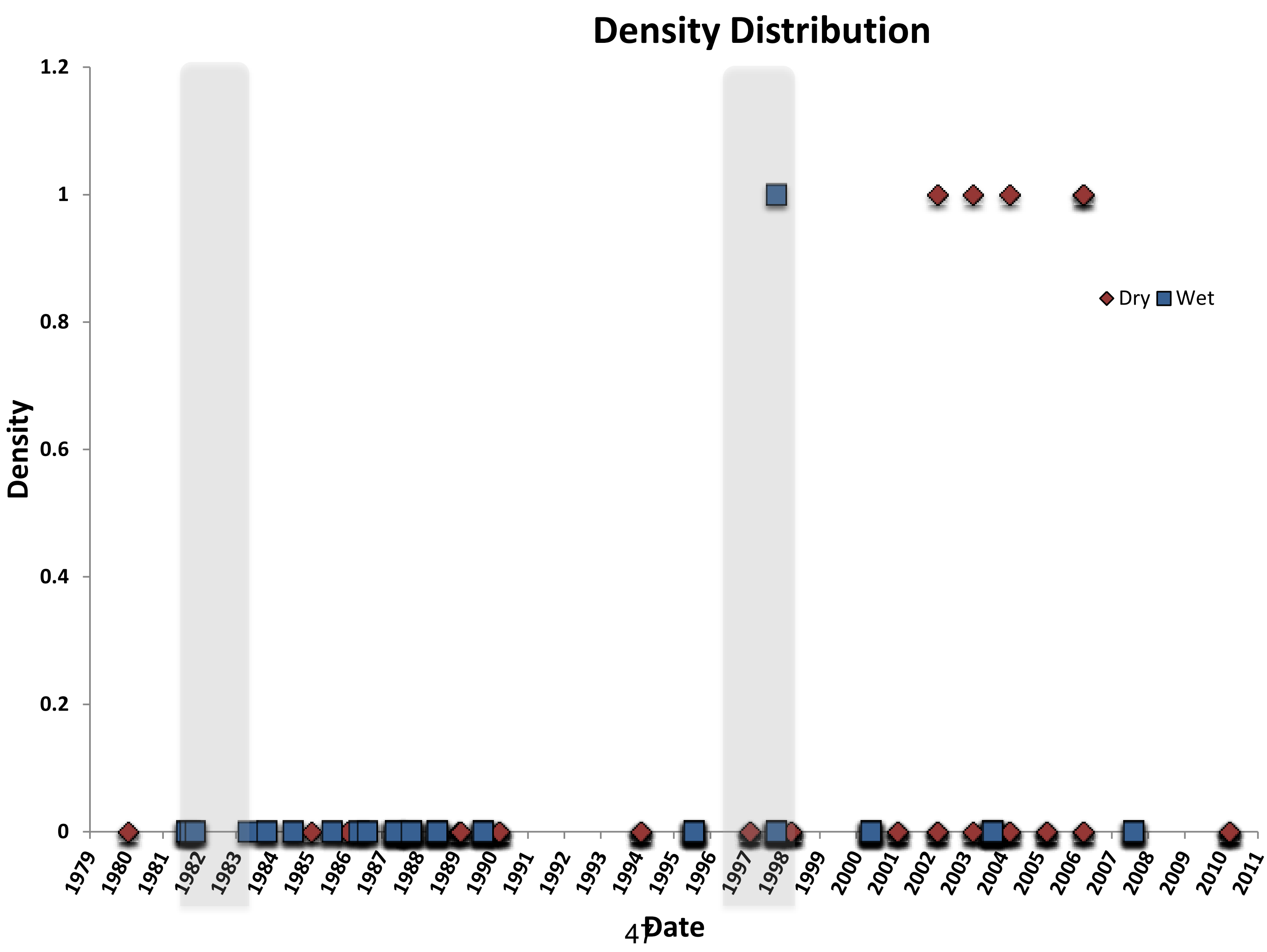
Epinephelus labriformis

Starry grouper

Max. size: 60 cm

Trophic group: Carnivore



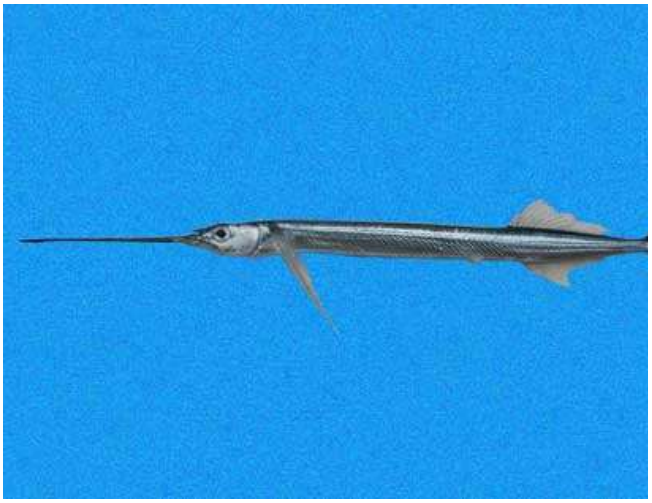


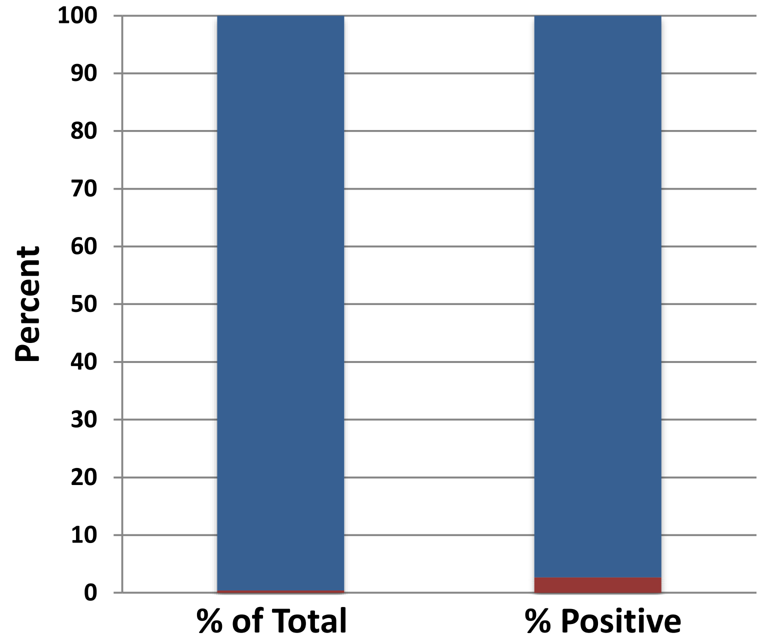
Euleptorhamphus viridis

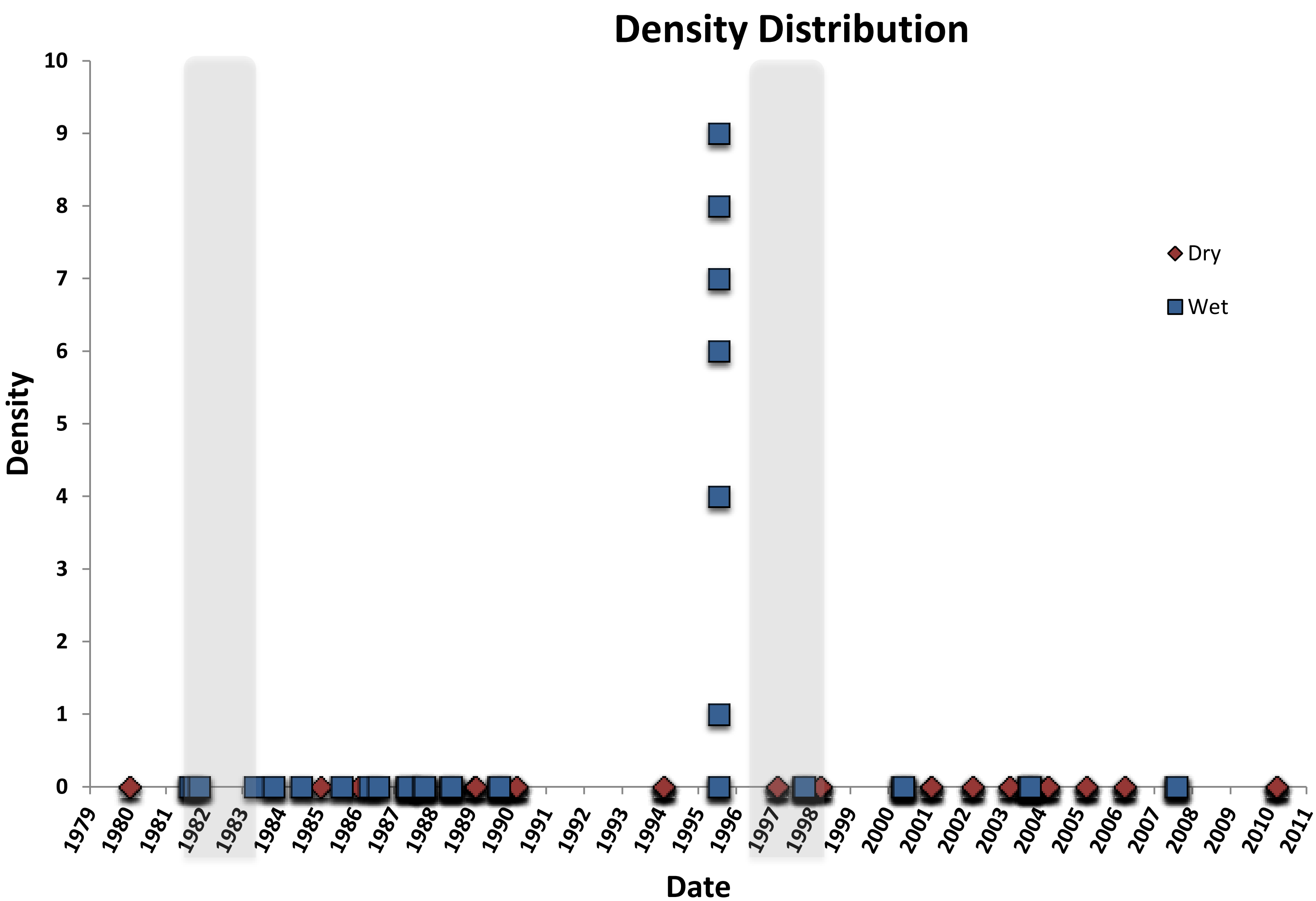
Ribbon halfbeak

Max. size: 53 cm

Trophic group: Planktivore







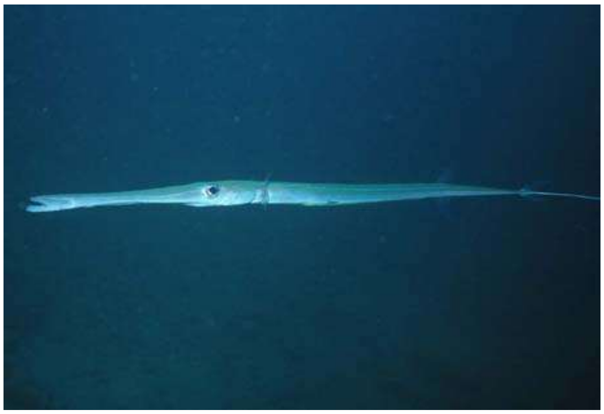
Fistularia commersonni

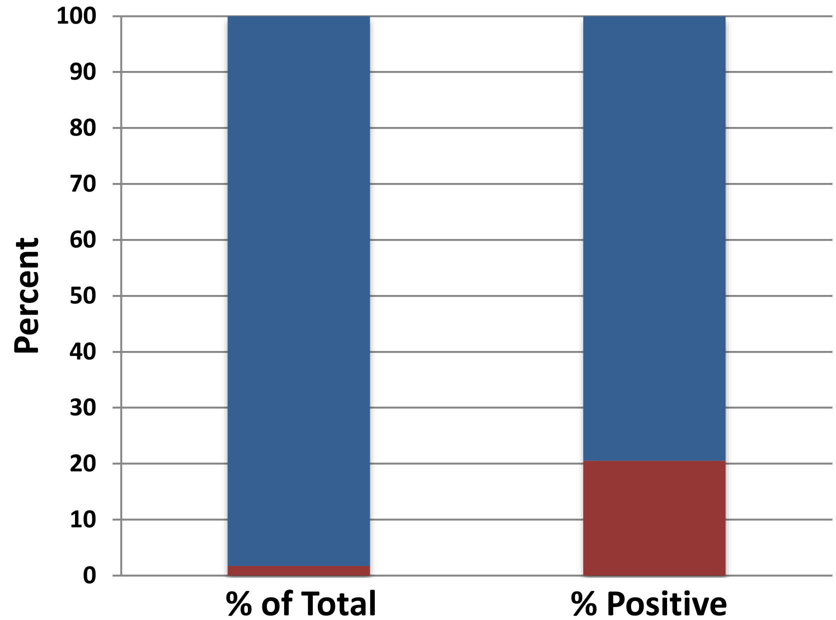
Blue-spotted/reef

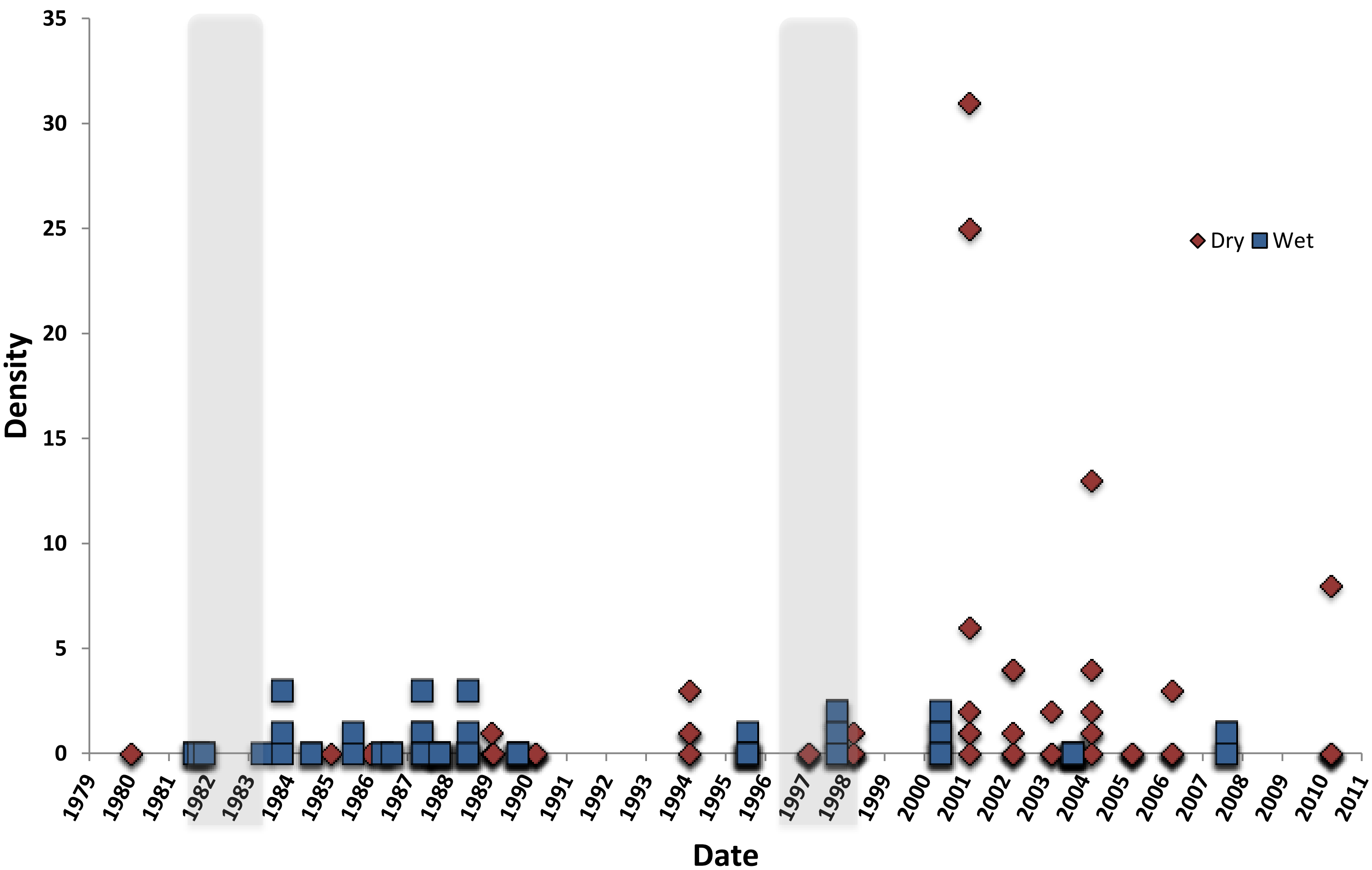
cornetfish

Max. size: 70 cm

Trophic group: Carnivore





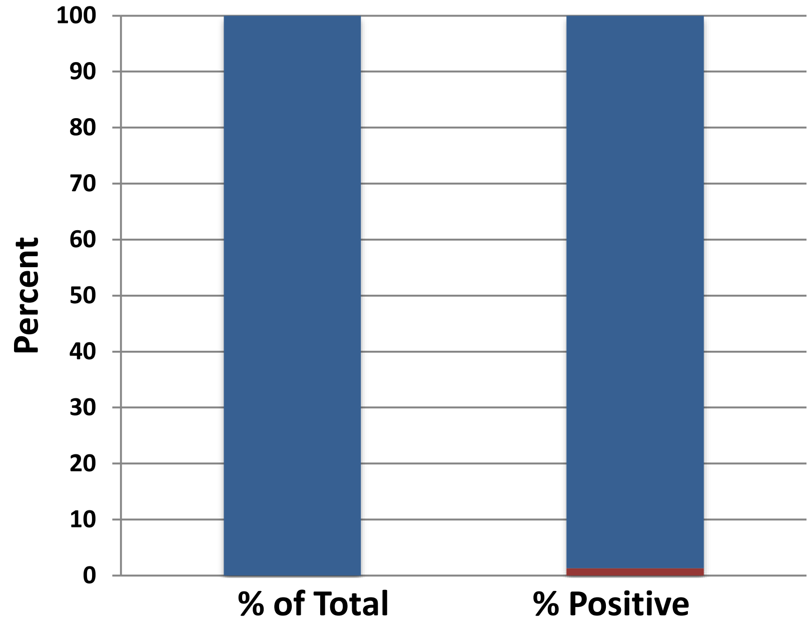


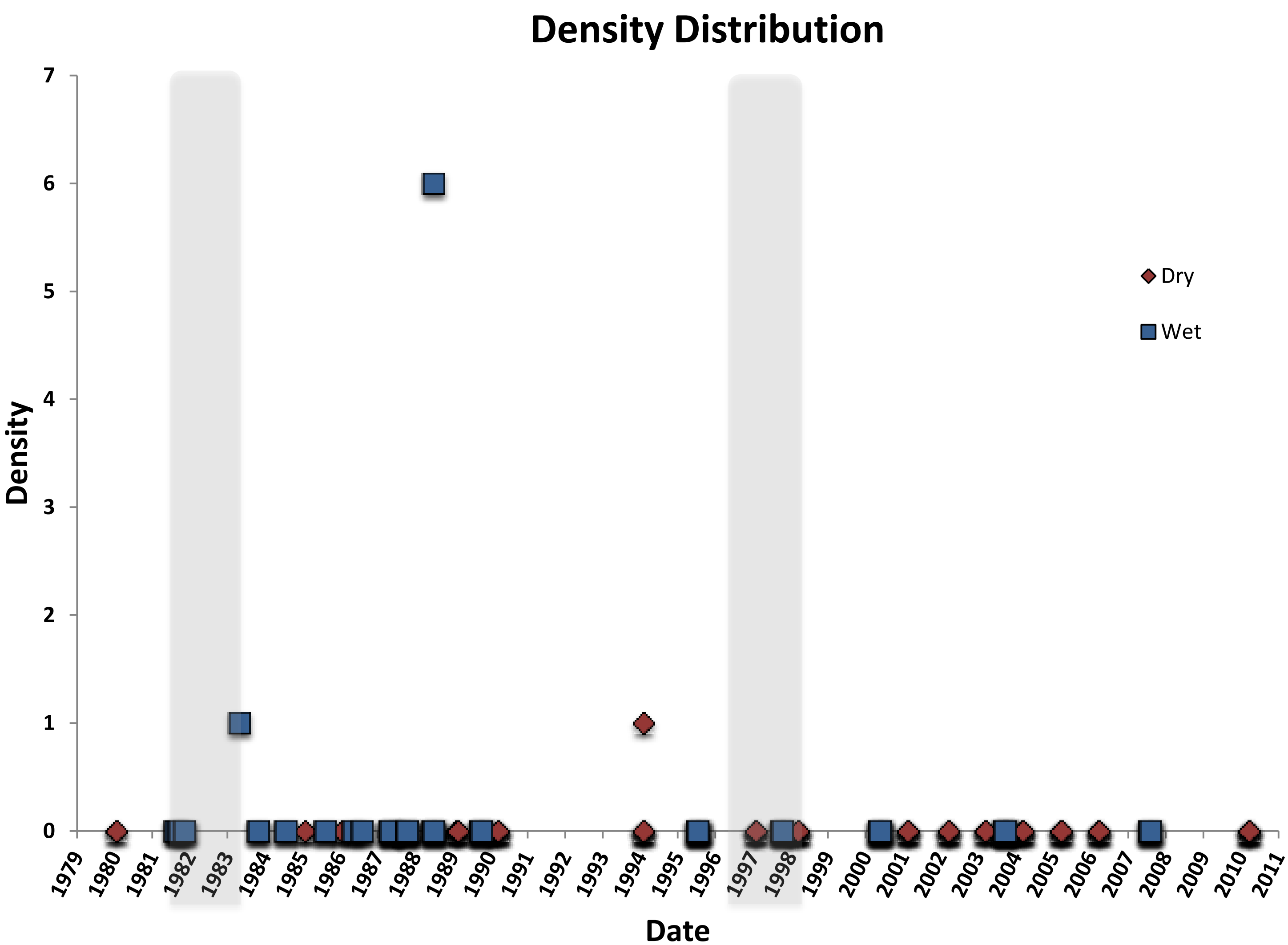
Gnathanodon speciosus

Golden jack

Max. size: 120 cm

Trophic group: Carnivore



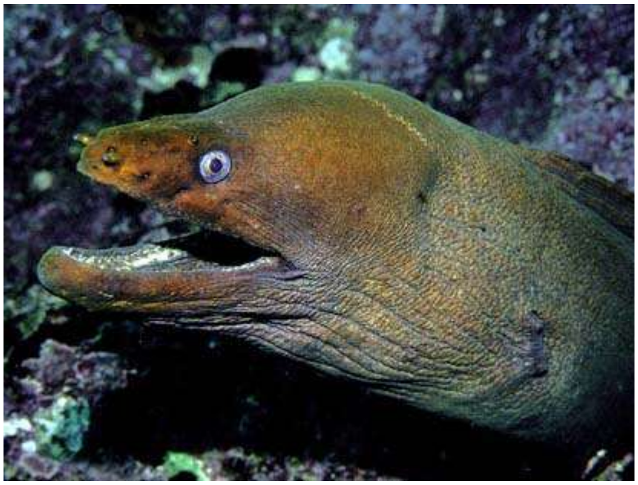


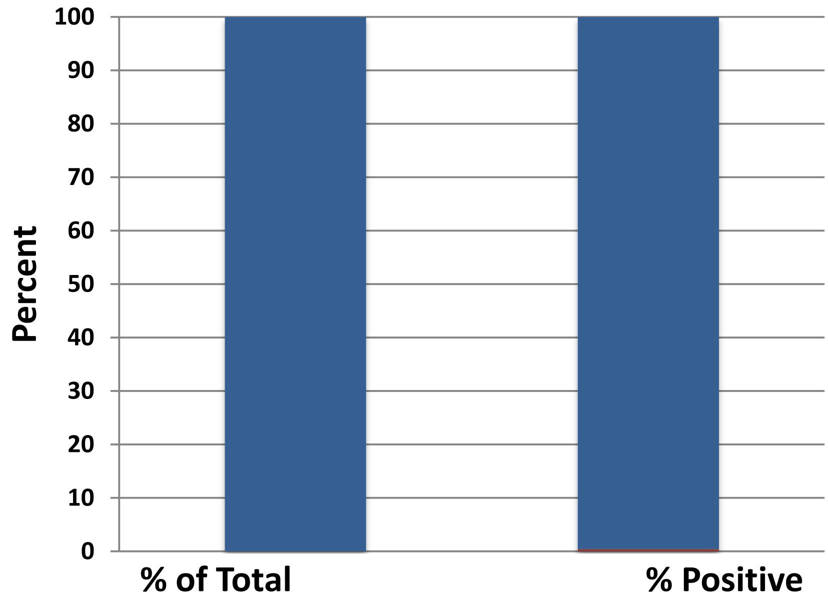
Gymnothorax castaneus

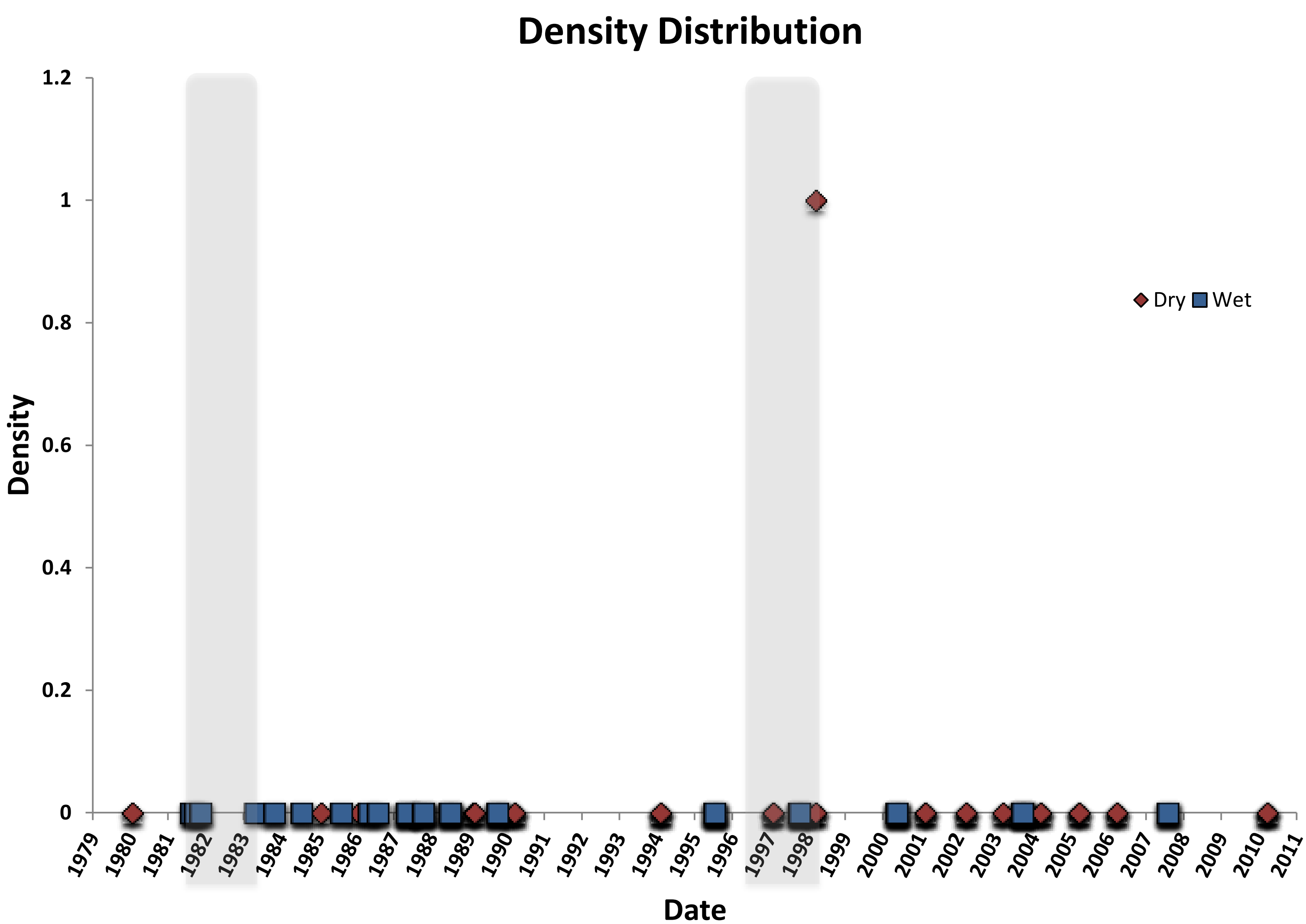
Panamic green moray

Max. size: 150 cm

Trophic group: Carnivore





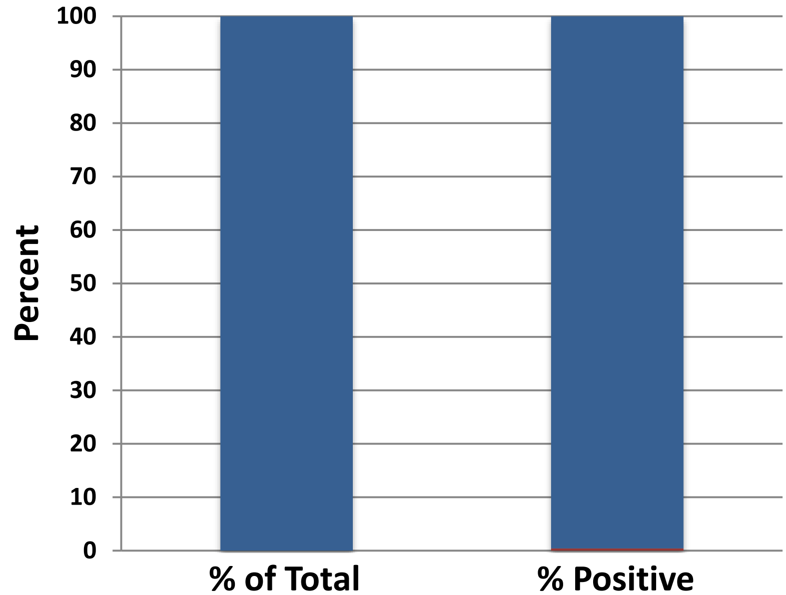


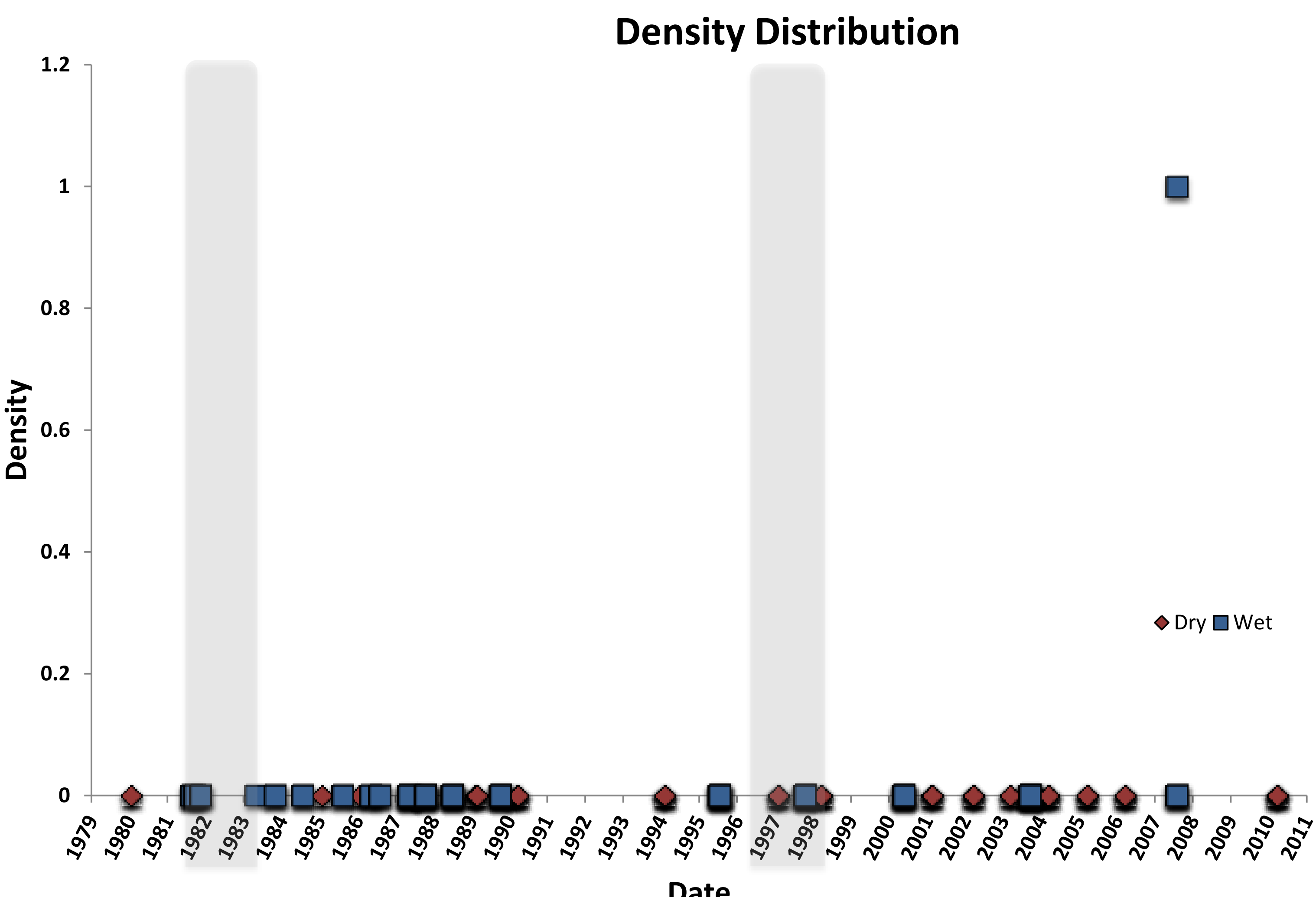
Gymnothorax undulatus

Undulated moray

Max. size: 150 cm

Trophic group: Carnivore



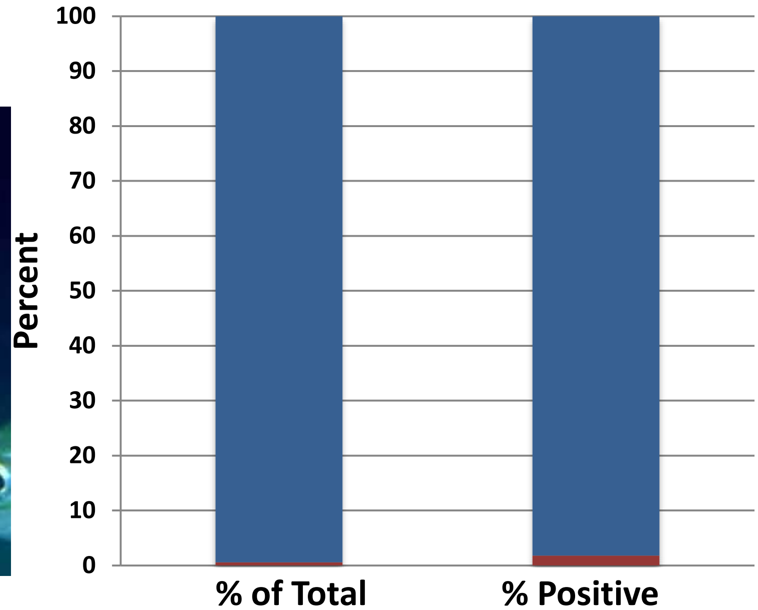


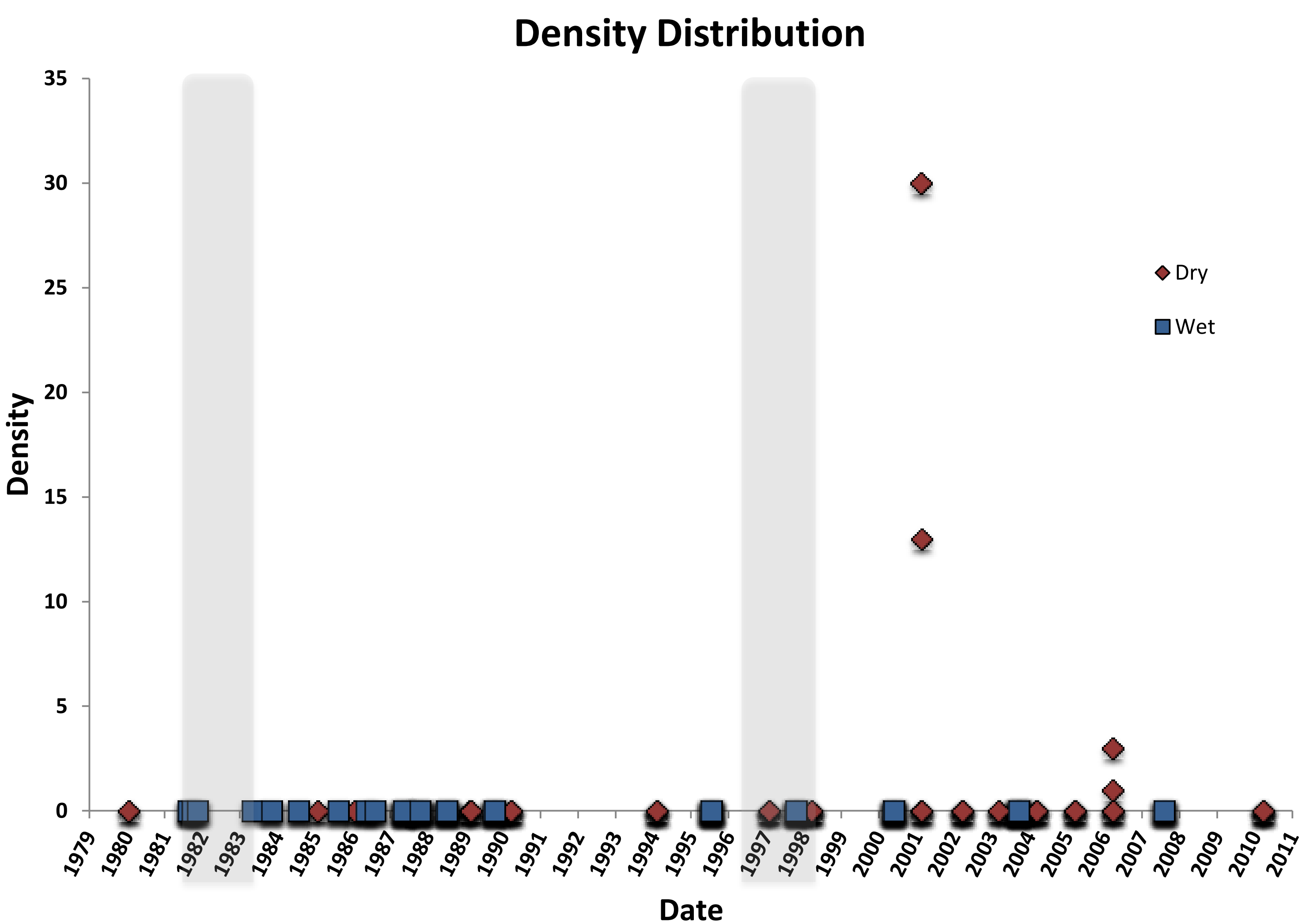
Haemulon steindachneri

Latin grunt

Max. size: 30 cm

Trophic group: Carnivore



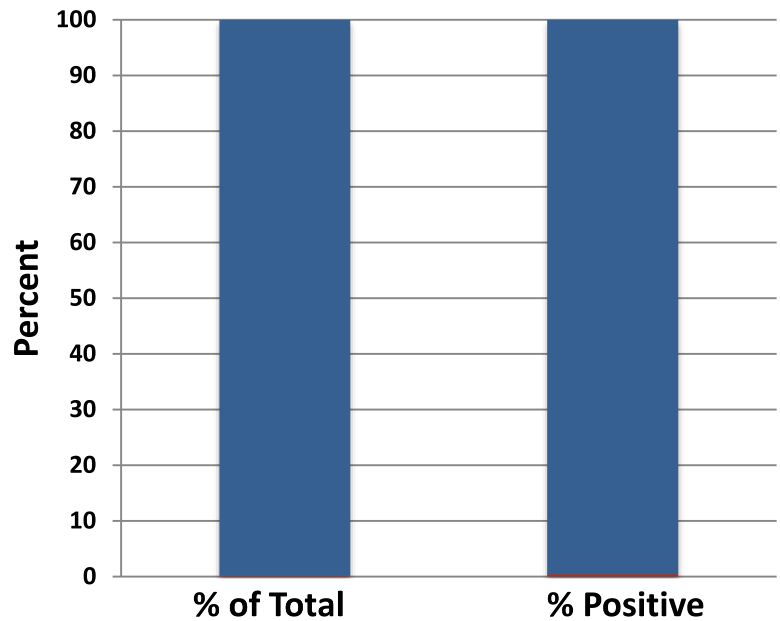


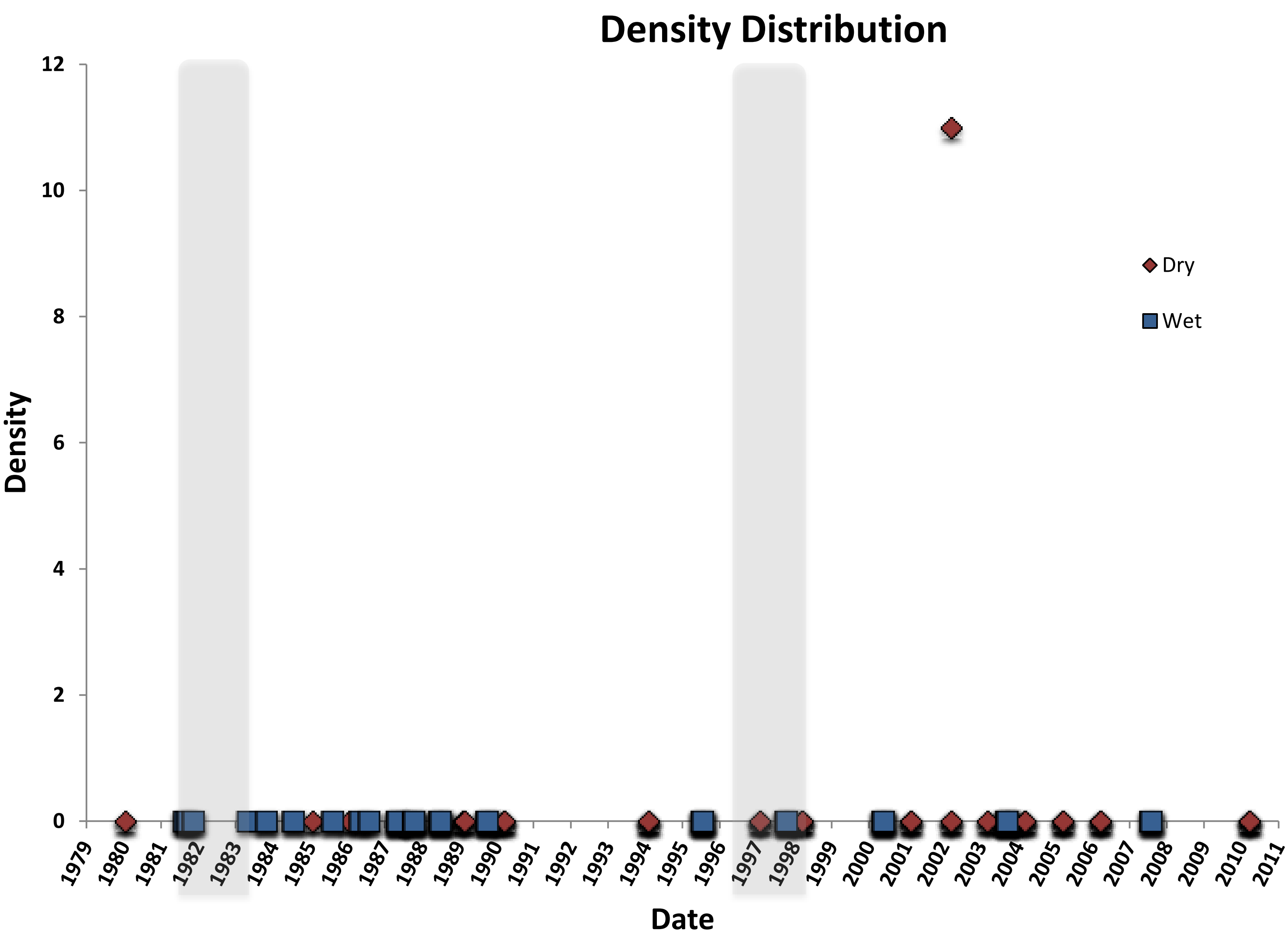
Haemulon maculicauda

Spot-tail grunt

Max. size: 30 cm

Trophic group: Invertivore



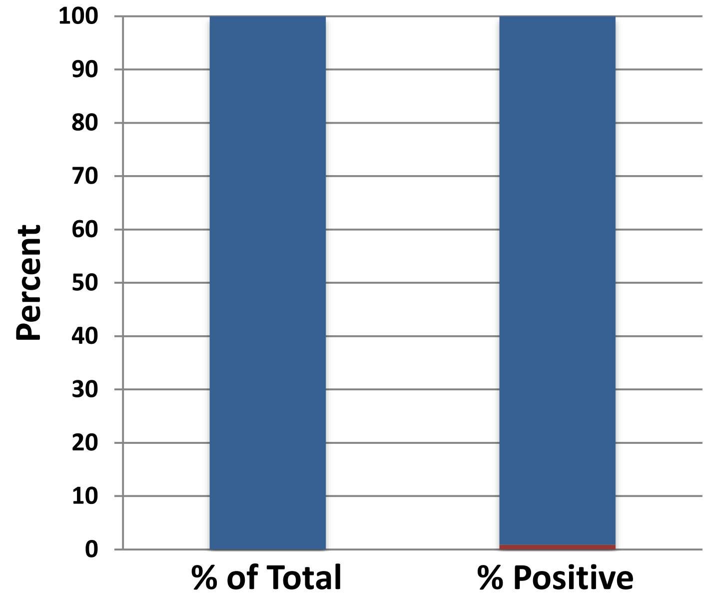


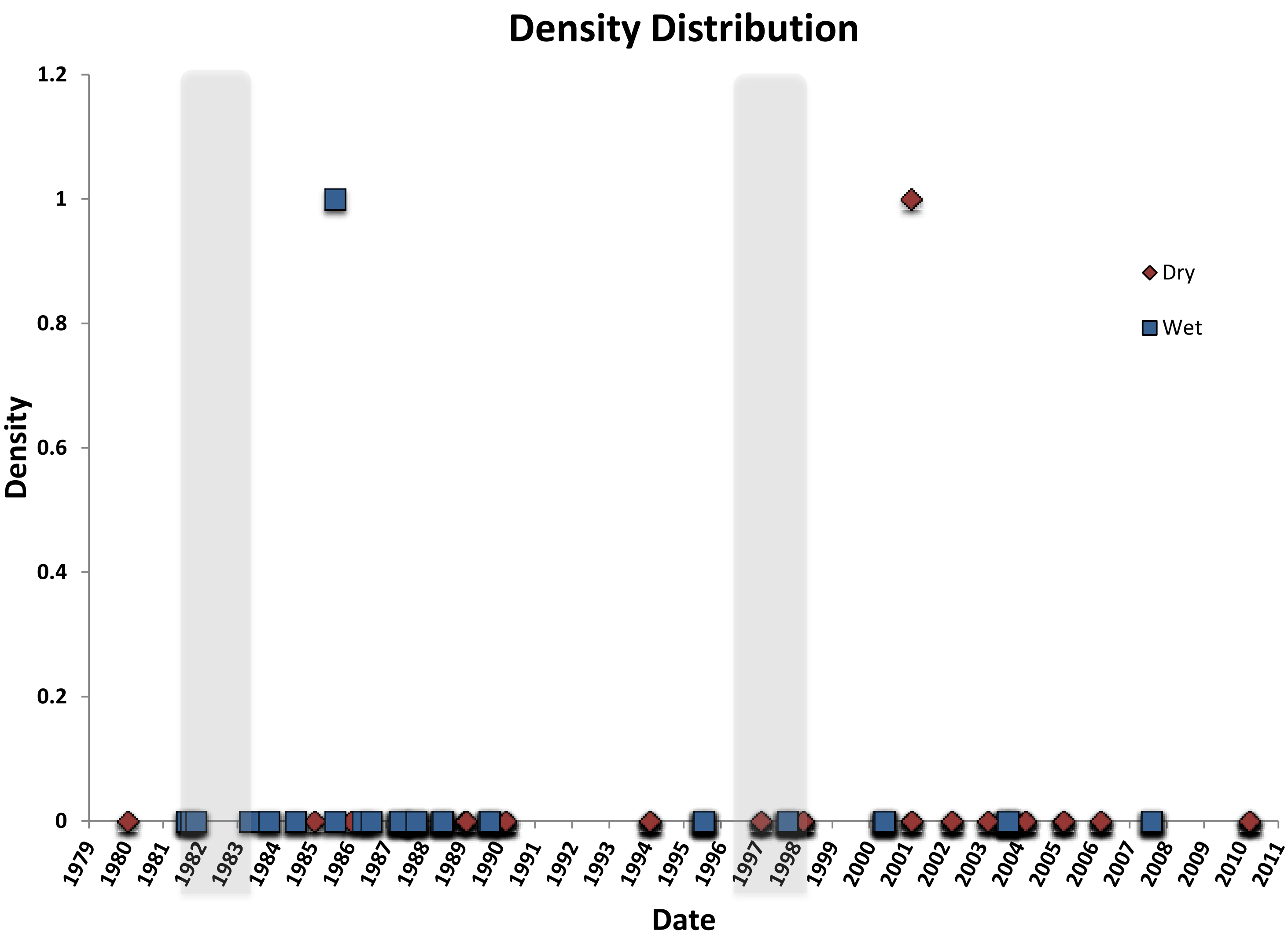
Halichoeres chierchiae

Wounded wrasse

Max. size: 20 cm

Trophic group: Invertivore



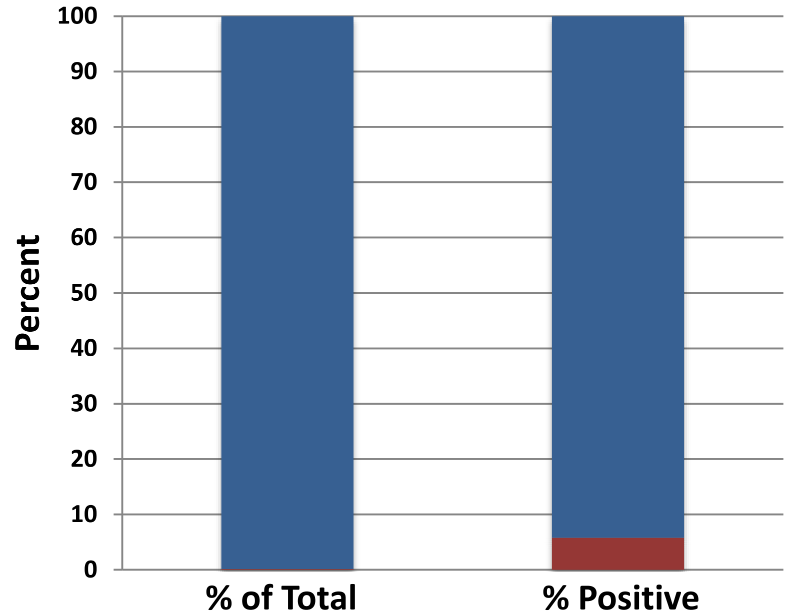


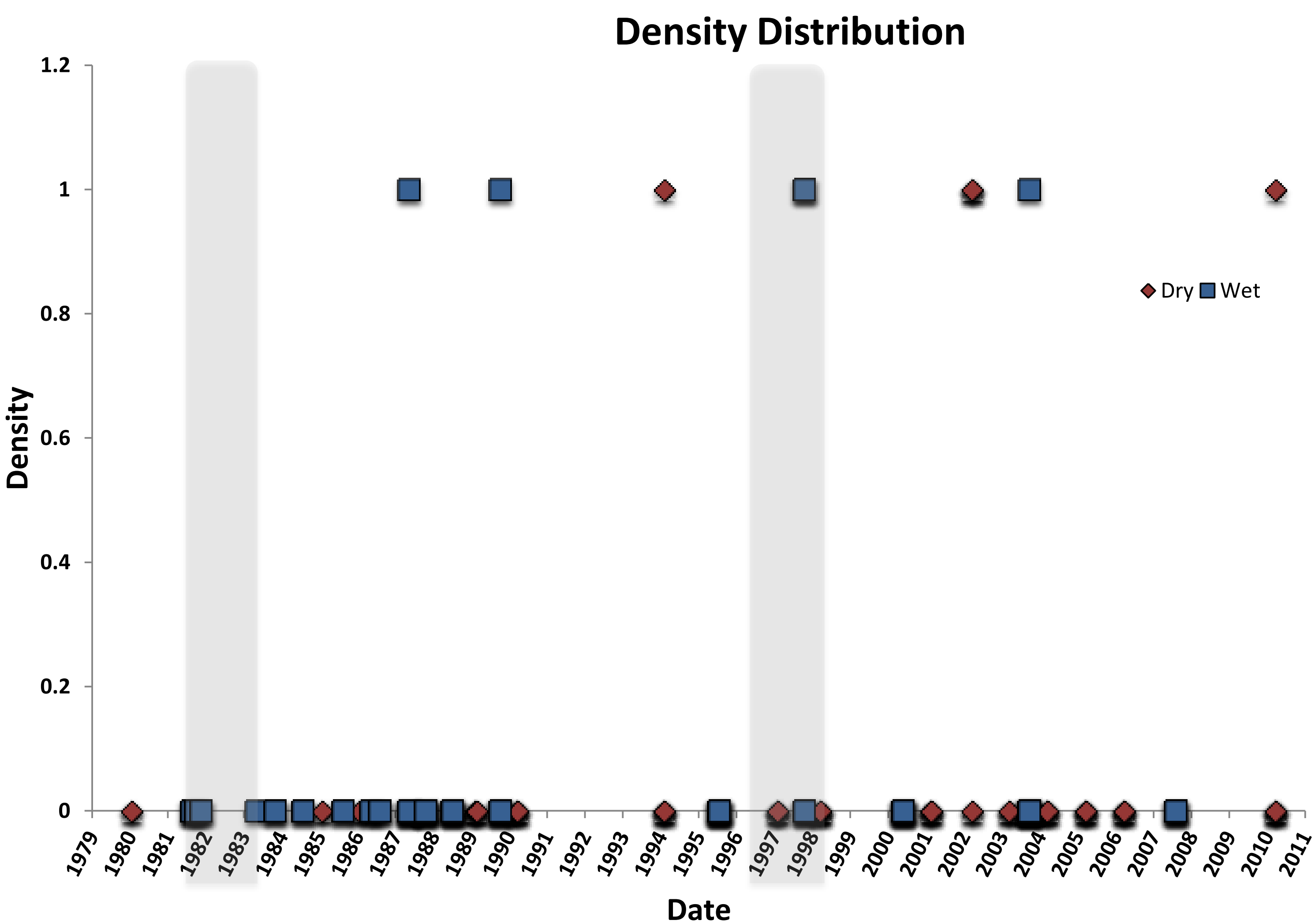
Halichoeres nicholsi

Spinster wrasse

Max. size: 38 cm

Trophic group: Invertivore



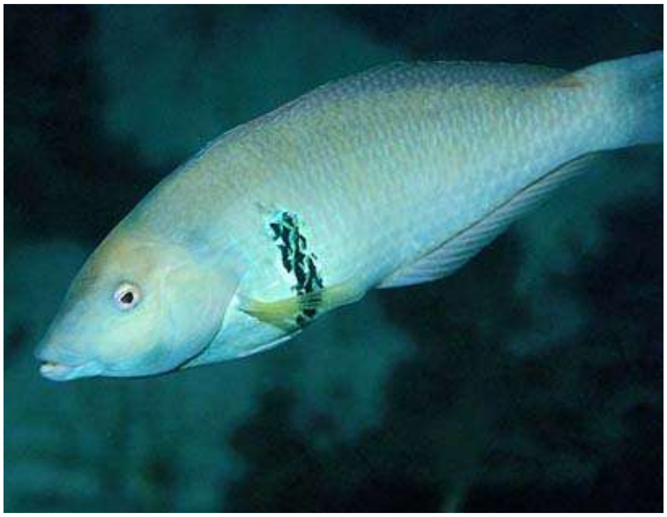


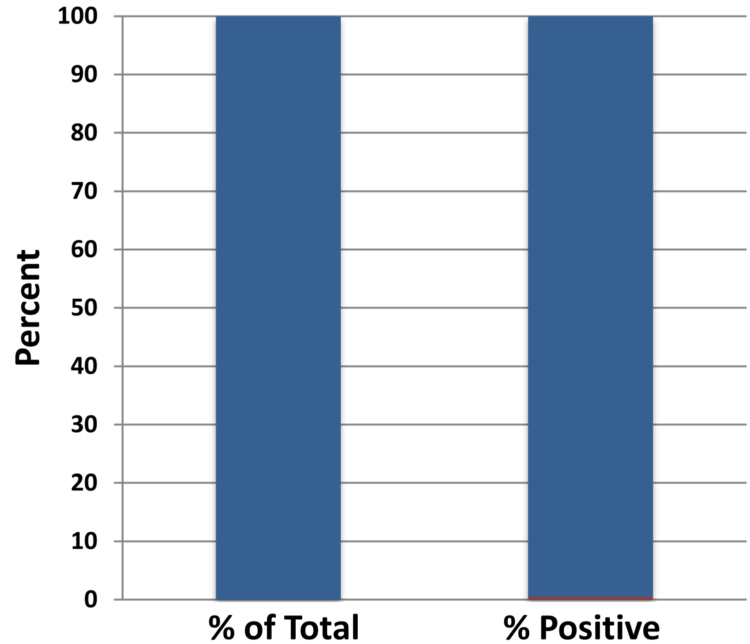
Halichoeres semicinctus

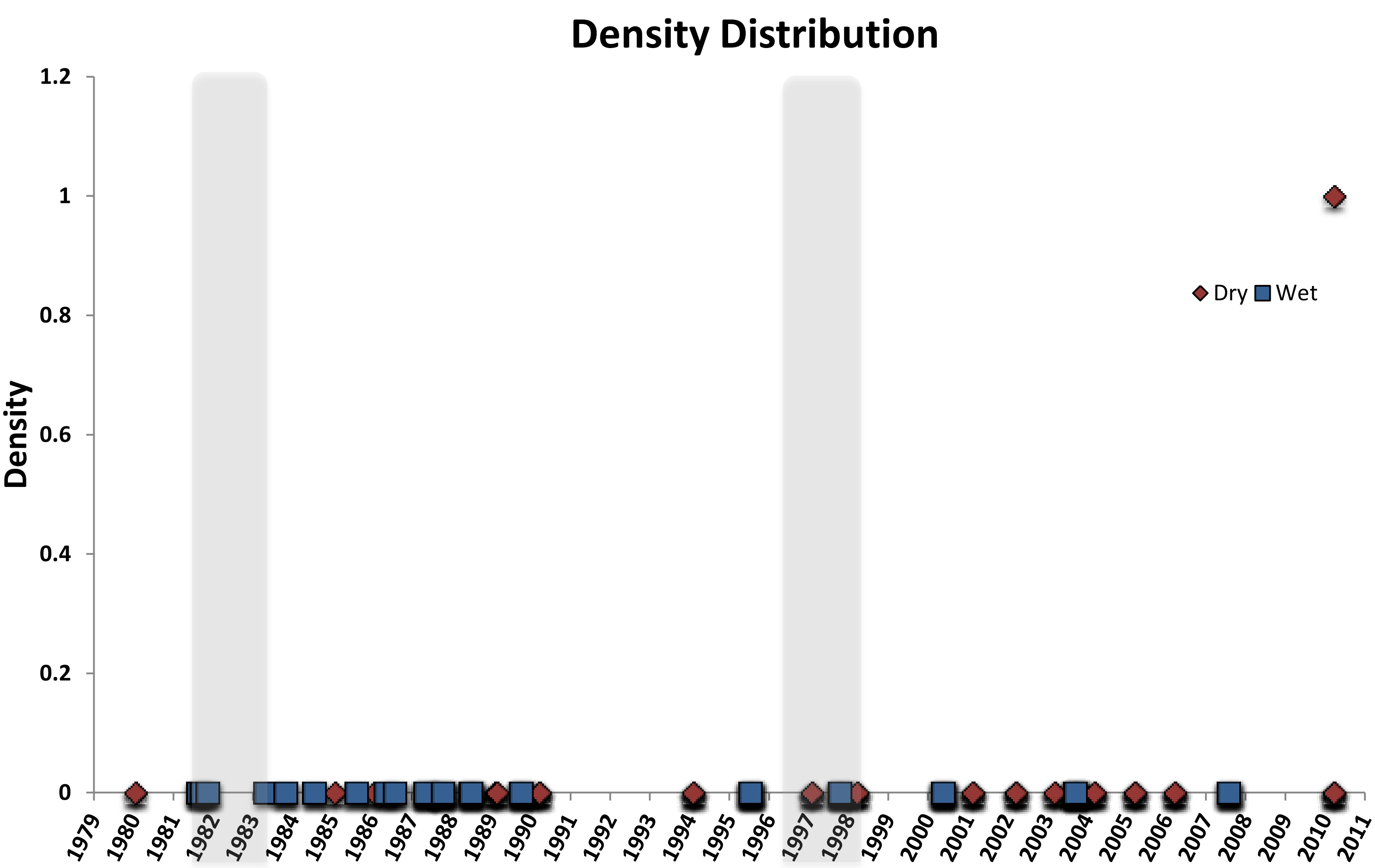
Rock wrasse

Max. size: 38 cm

Trophic group: Invertivore





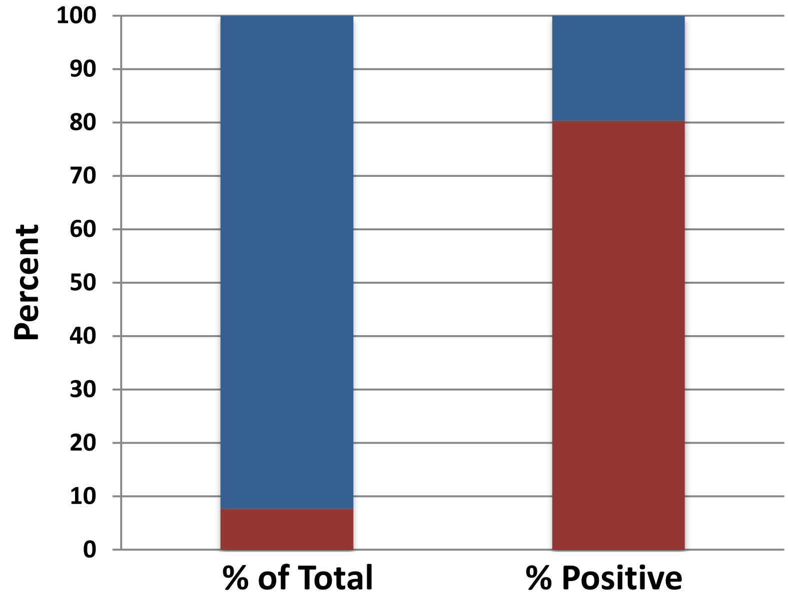


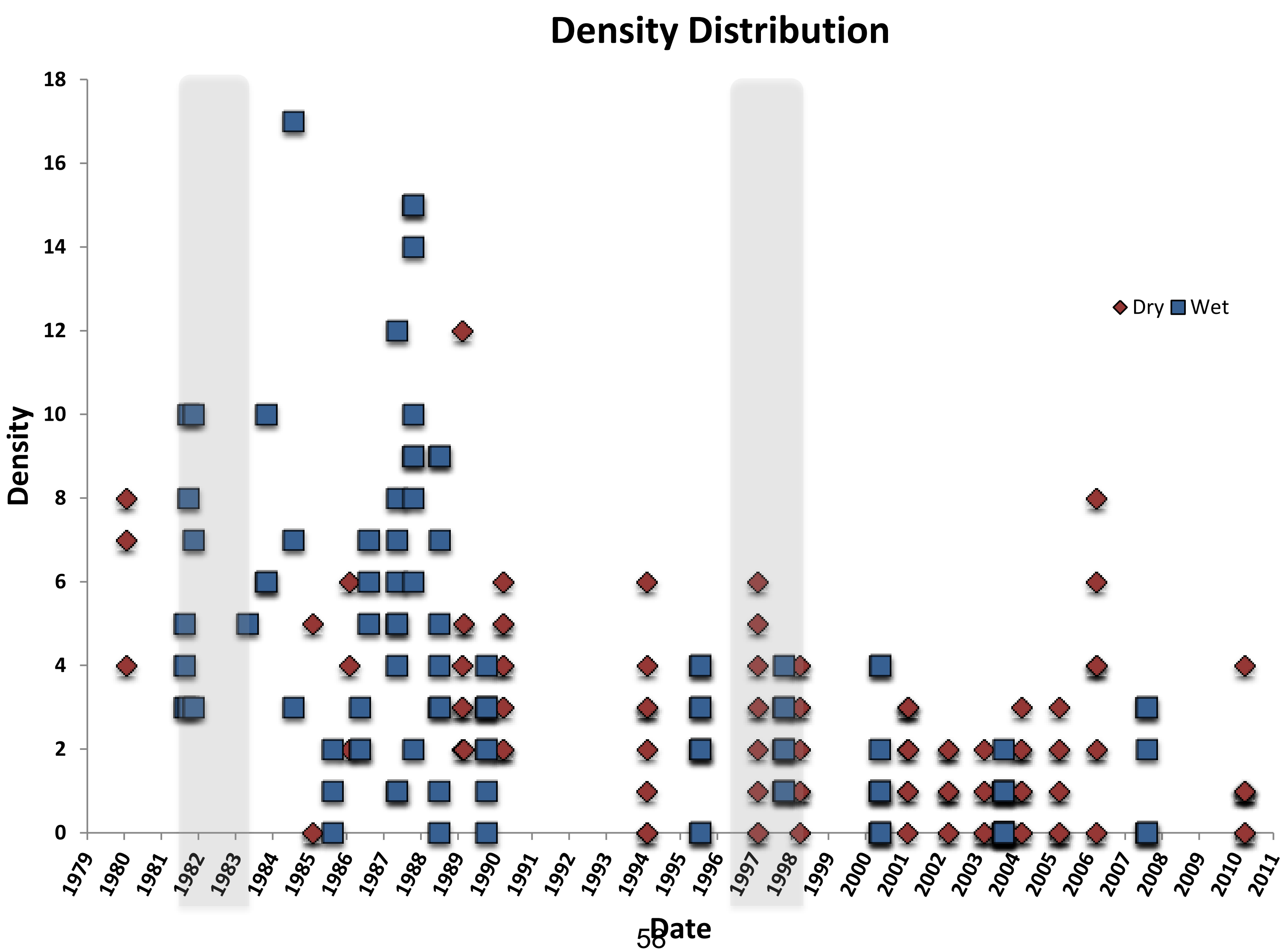
Holacanthus passer

King angelfish

Max. size: 36 cm

Trophic group: Omnivore



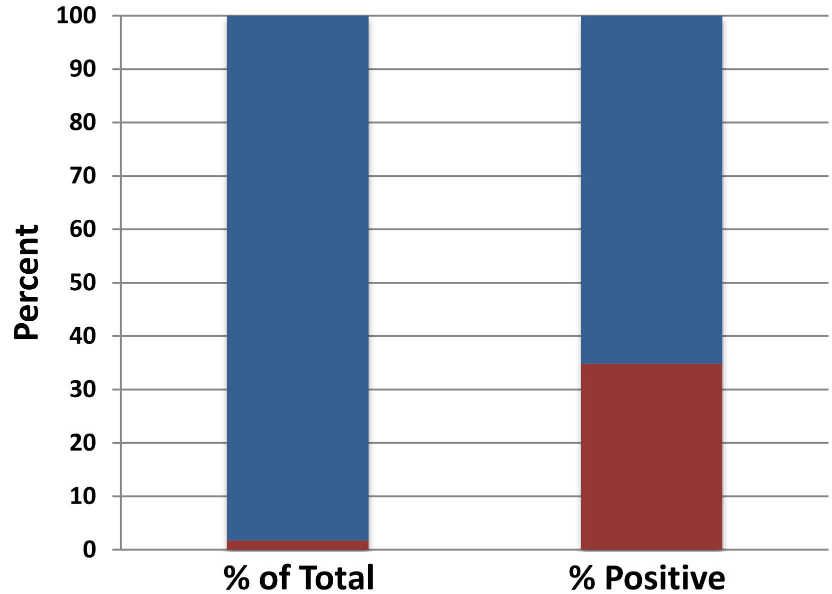


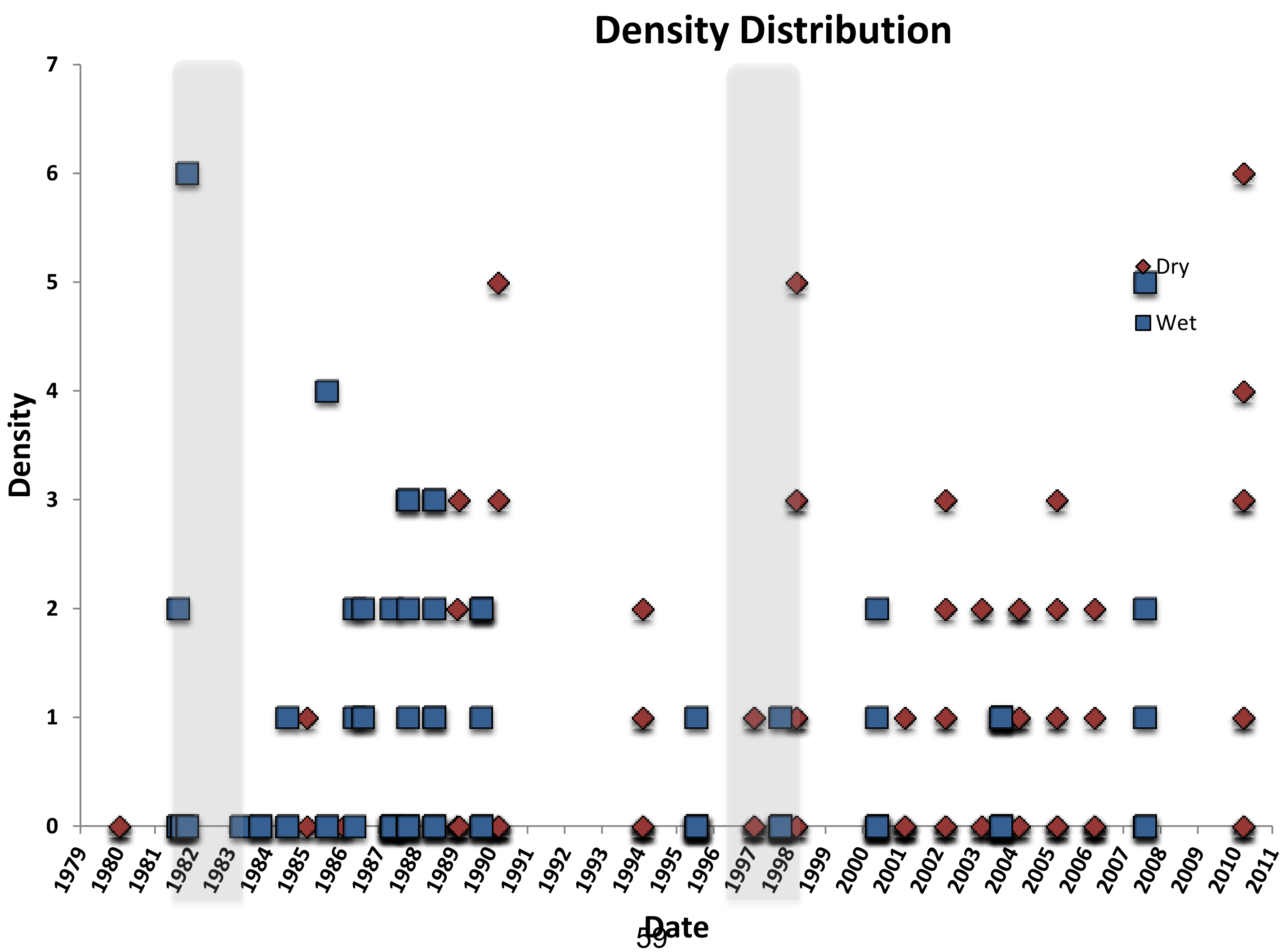
Johnrandallia nigrirostris

Blacknose butterflyfish

Max. size: 20 cm

Trophic group: Omnivore



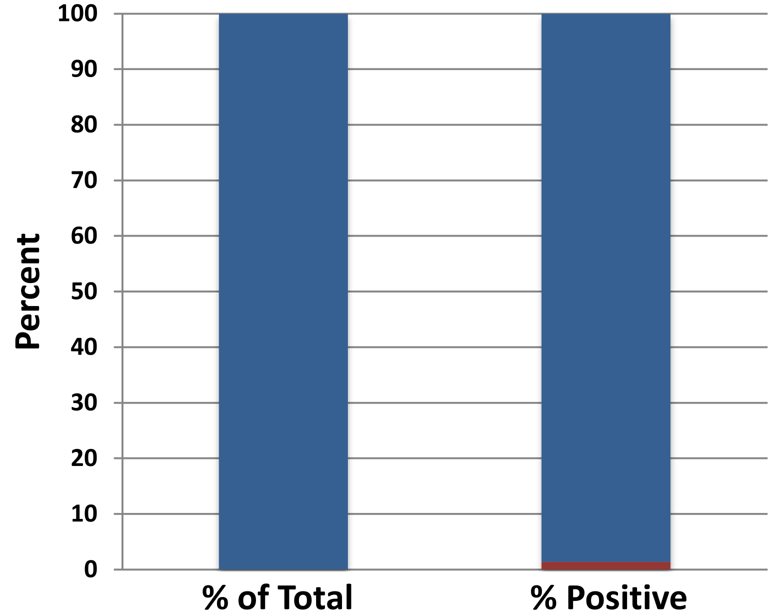


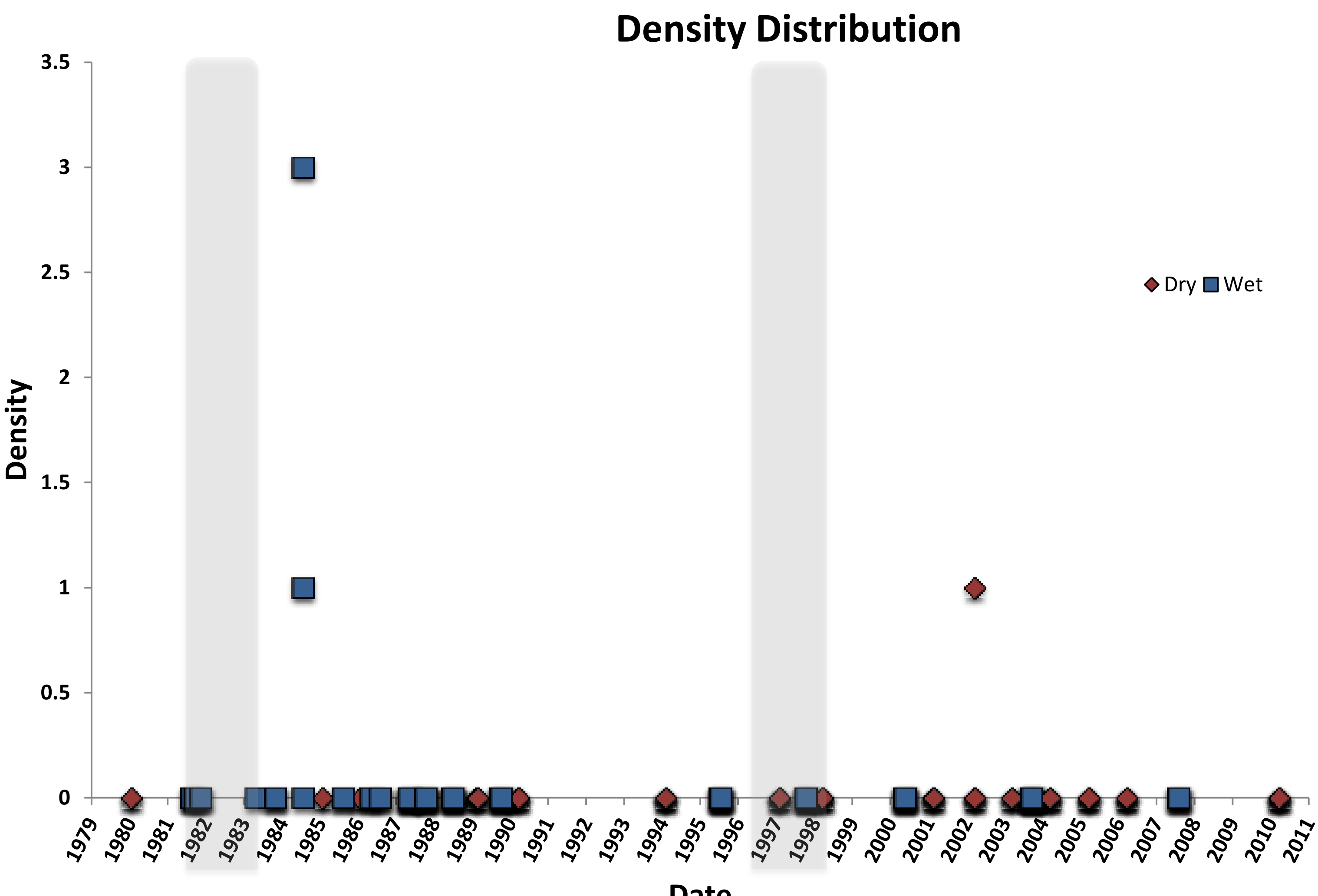
Kyphosus analogus

Striped sea-chub

Max. size: 45 cm

Trophic group: Omnivore (Planktivore, Herbivore)



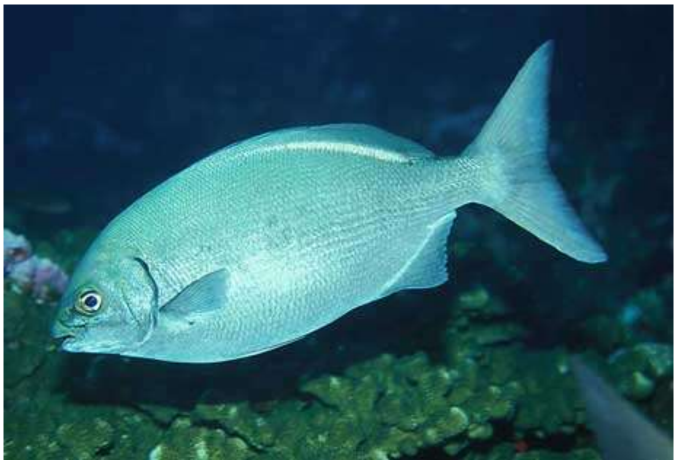


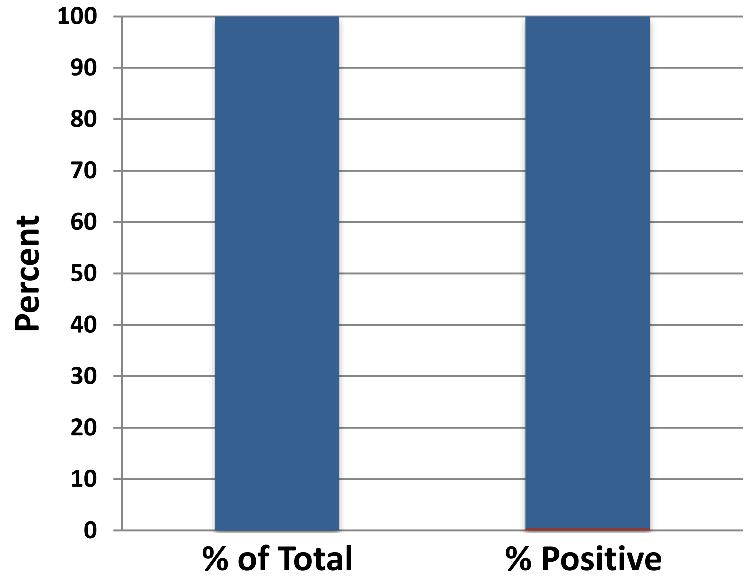
Kyphosus elegans

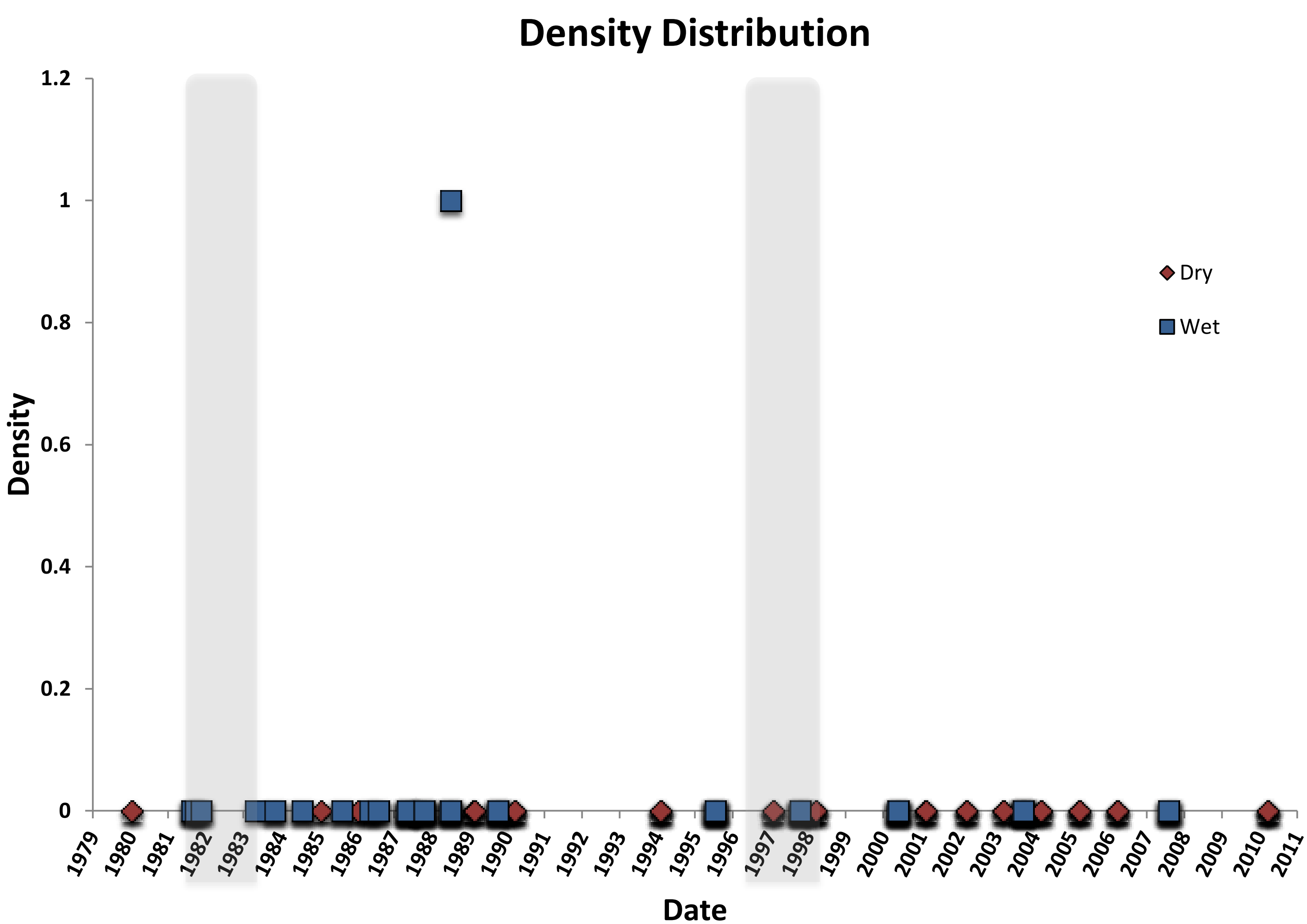
Cortez sea-chub

Max. size: 38 cm

Trophic group: Omnivore





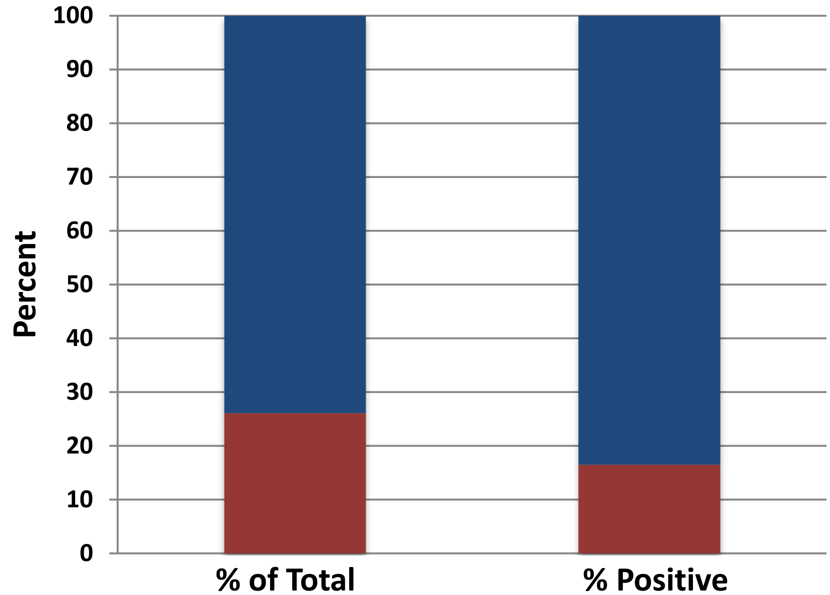


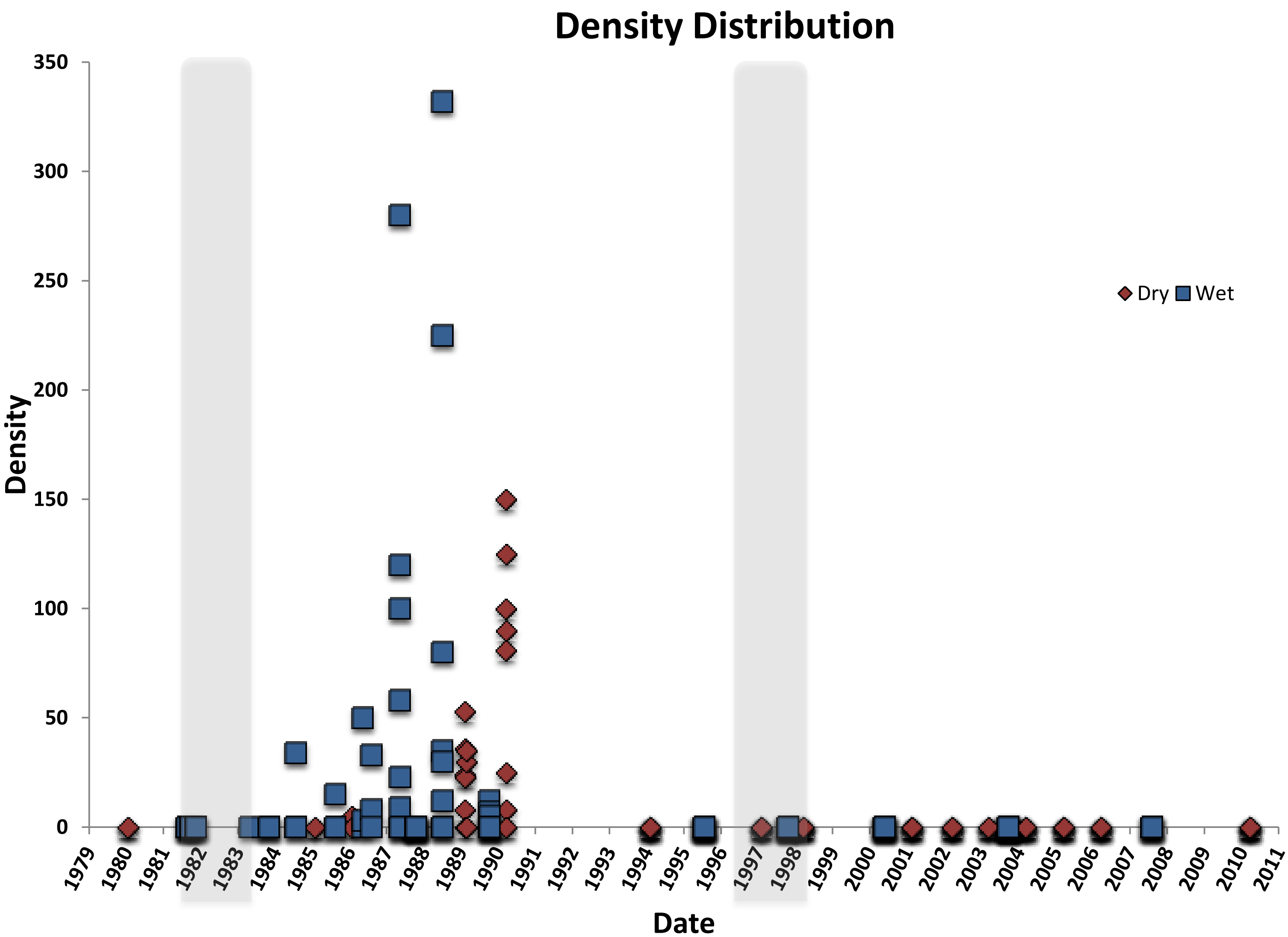
Lutjanus viridis

Blue and gold snapper

Max. size: 30 cm

Trophic group: Carnivore



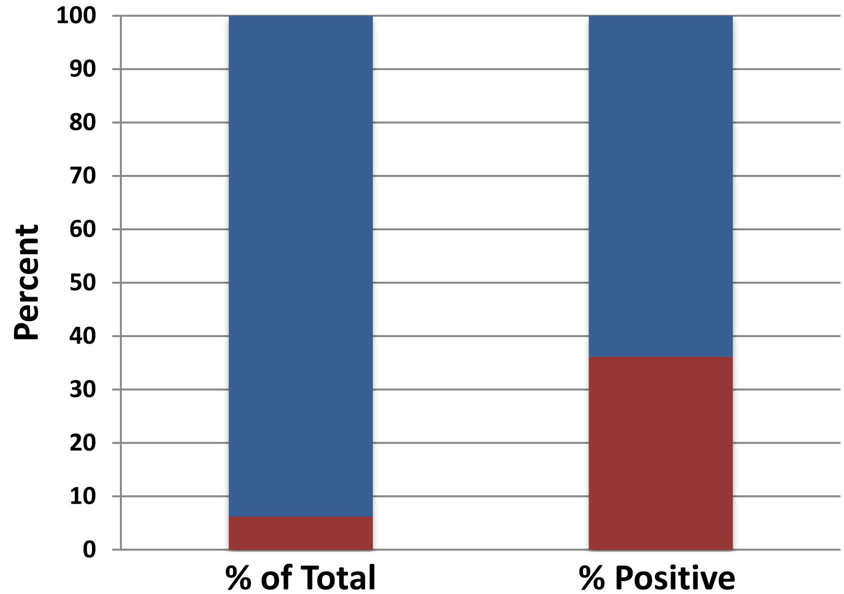


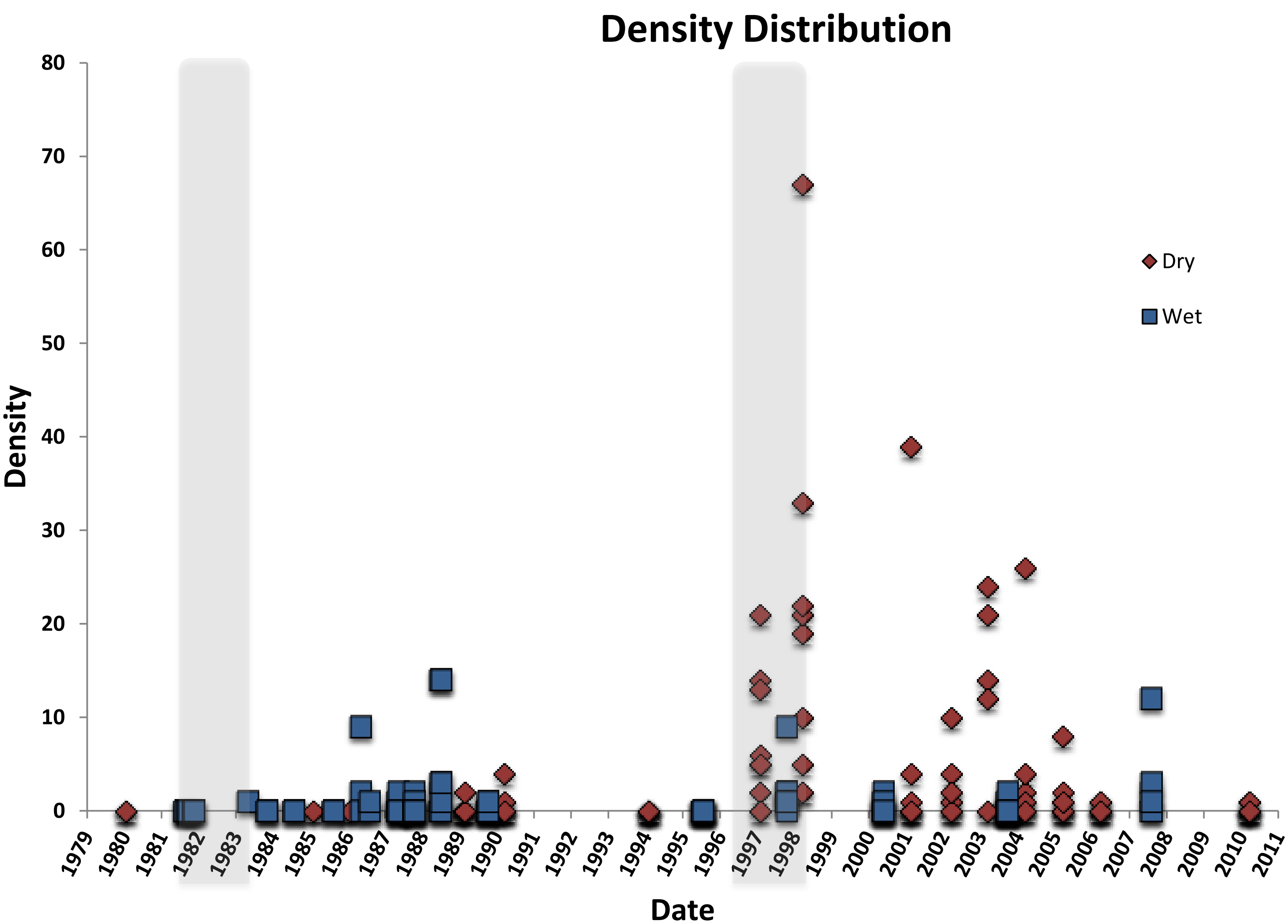
Lutjanus argentiventris

Yellow snapper

Max. size: 66 cm

Trophic group: Carnivore



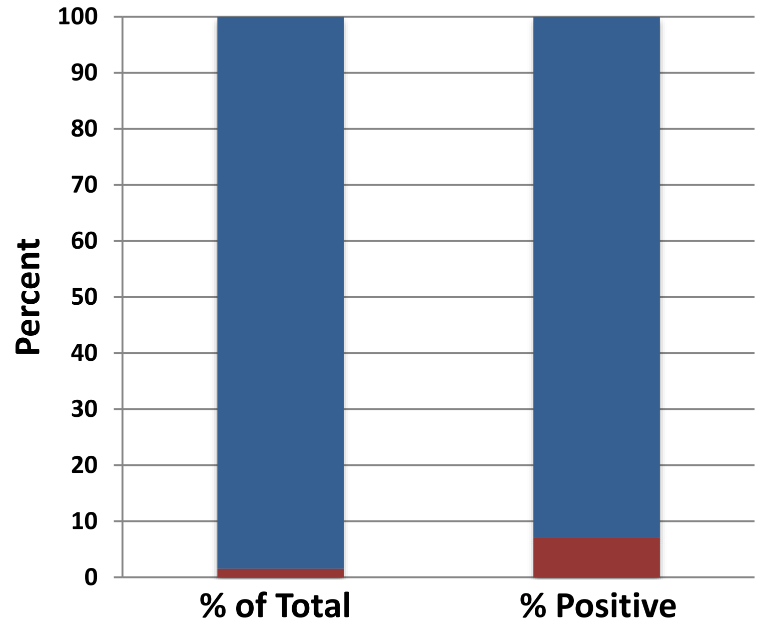


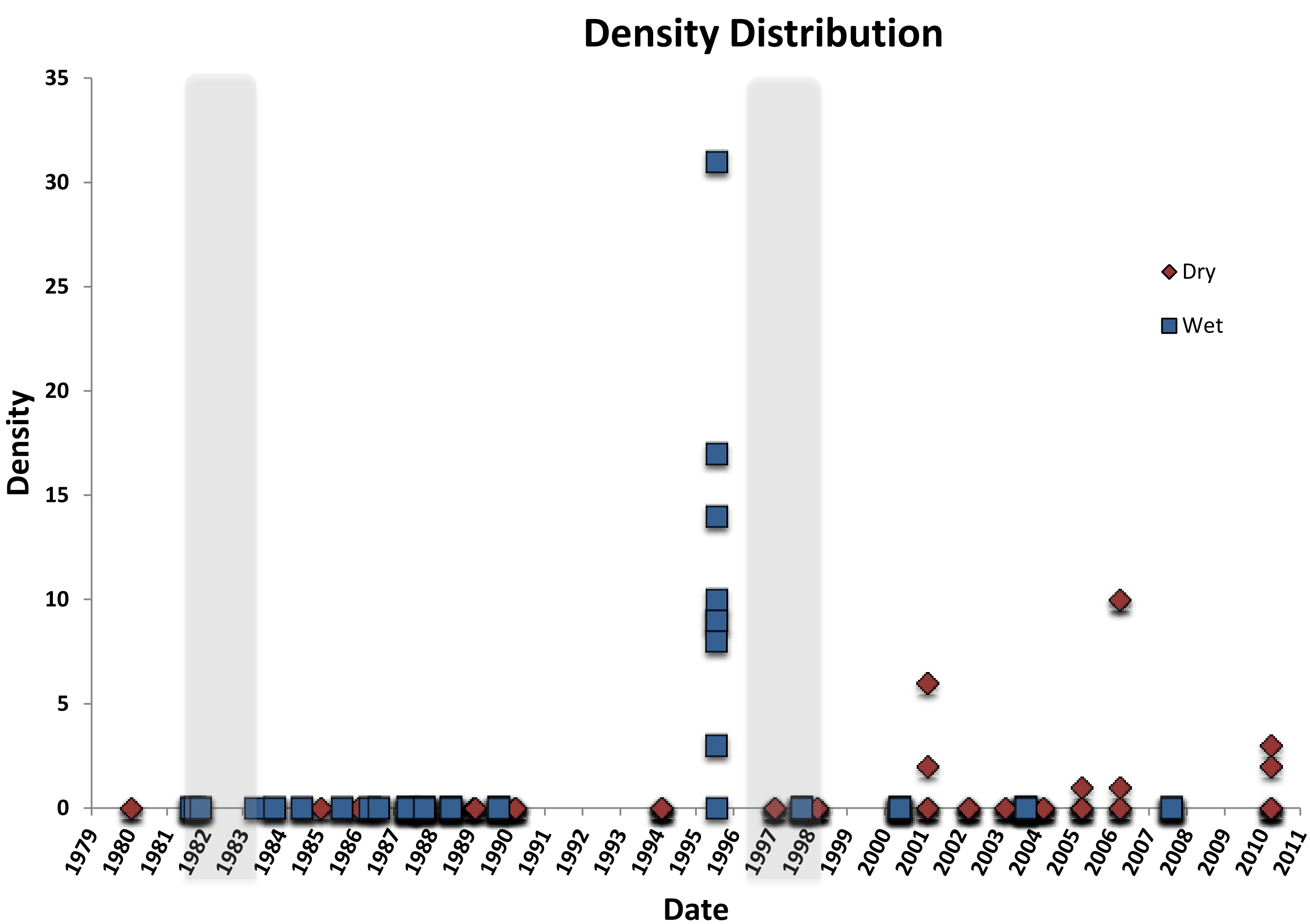
Lutjanus guttatus

Spotted rose snapper

Max. size: 80 cm, commonly 40 cm

Trophic group: Carnivore



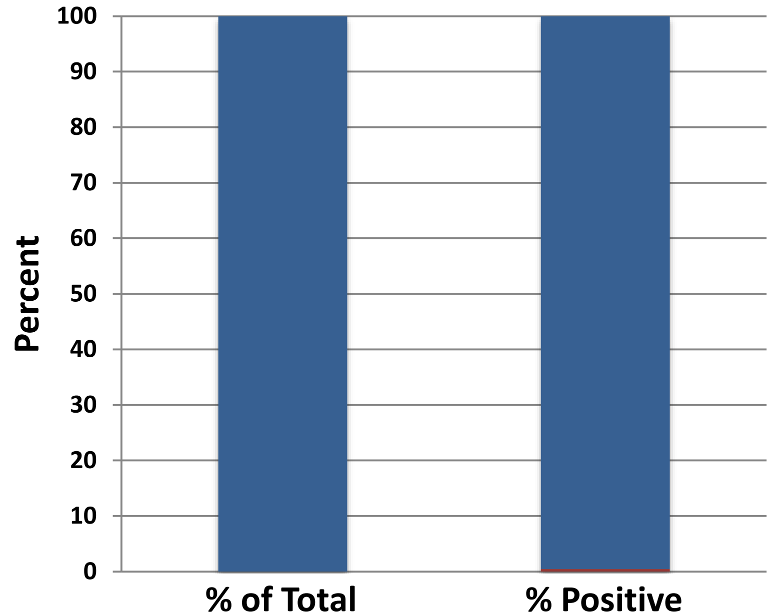


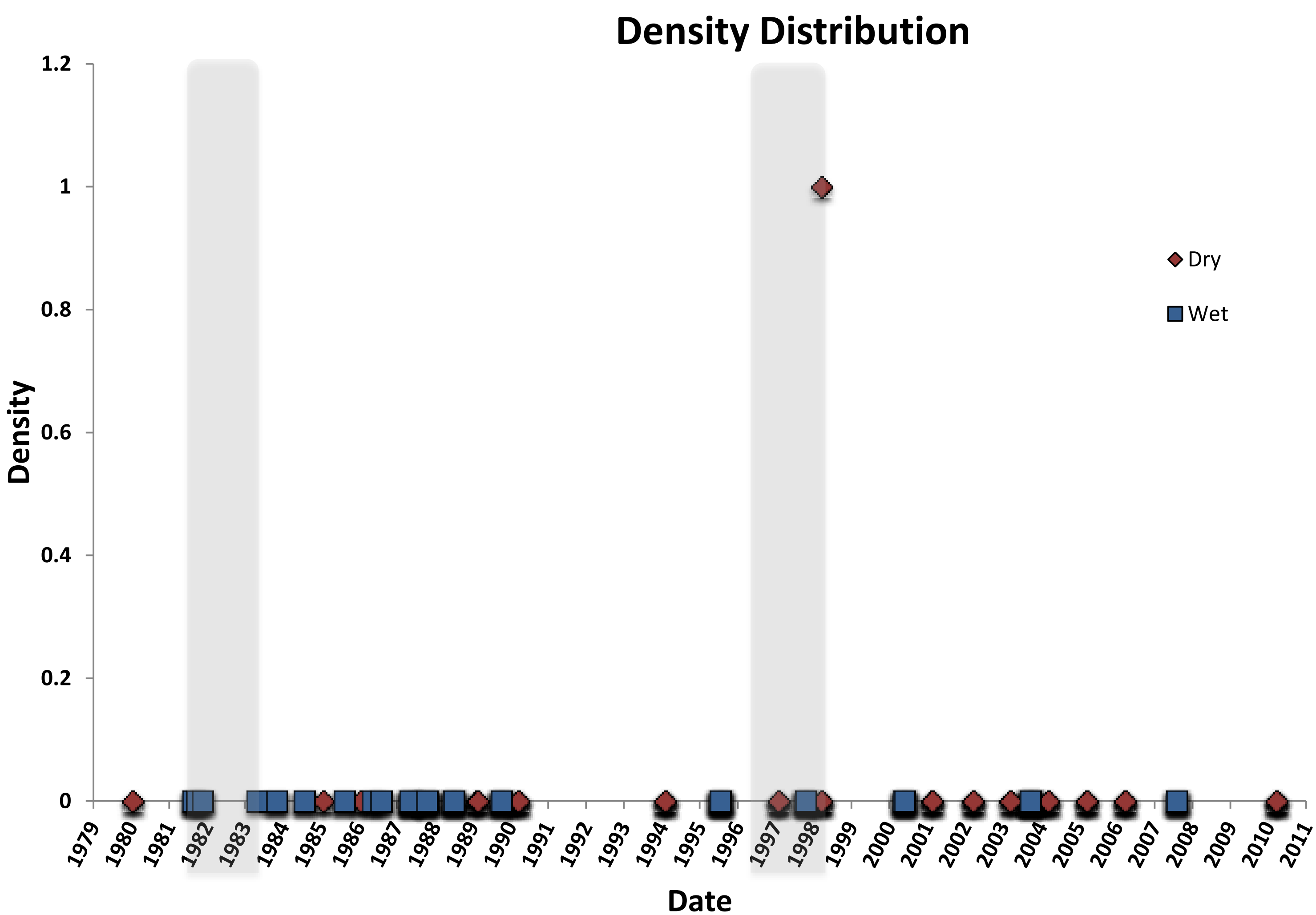
Lutjanus novemfaciatus

Pacific cubera snapper

Max. size: 170 cm

Trophic group: Carnivore



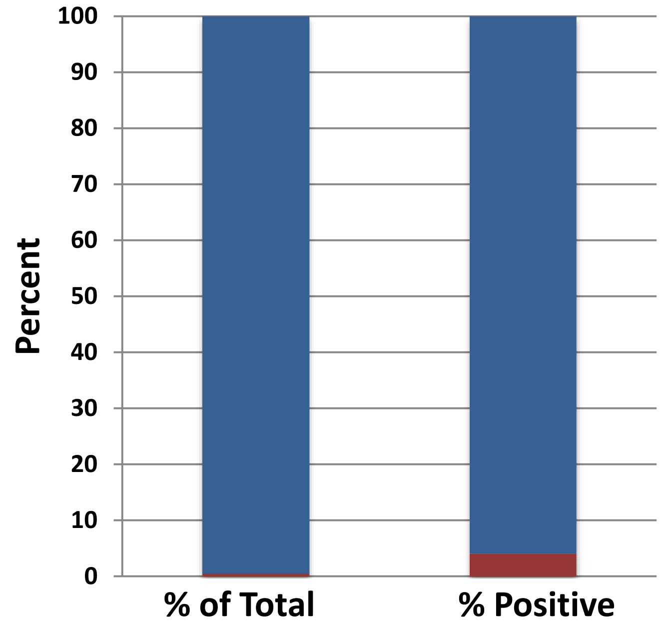


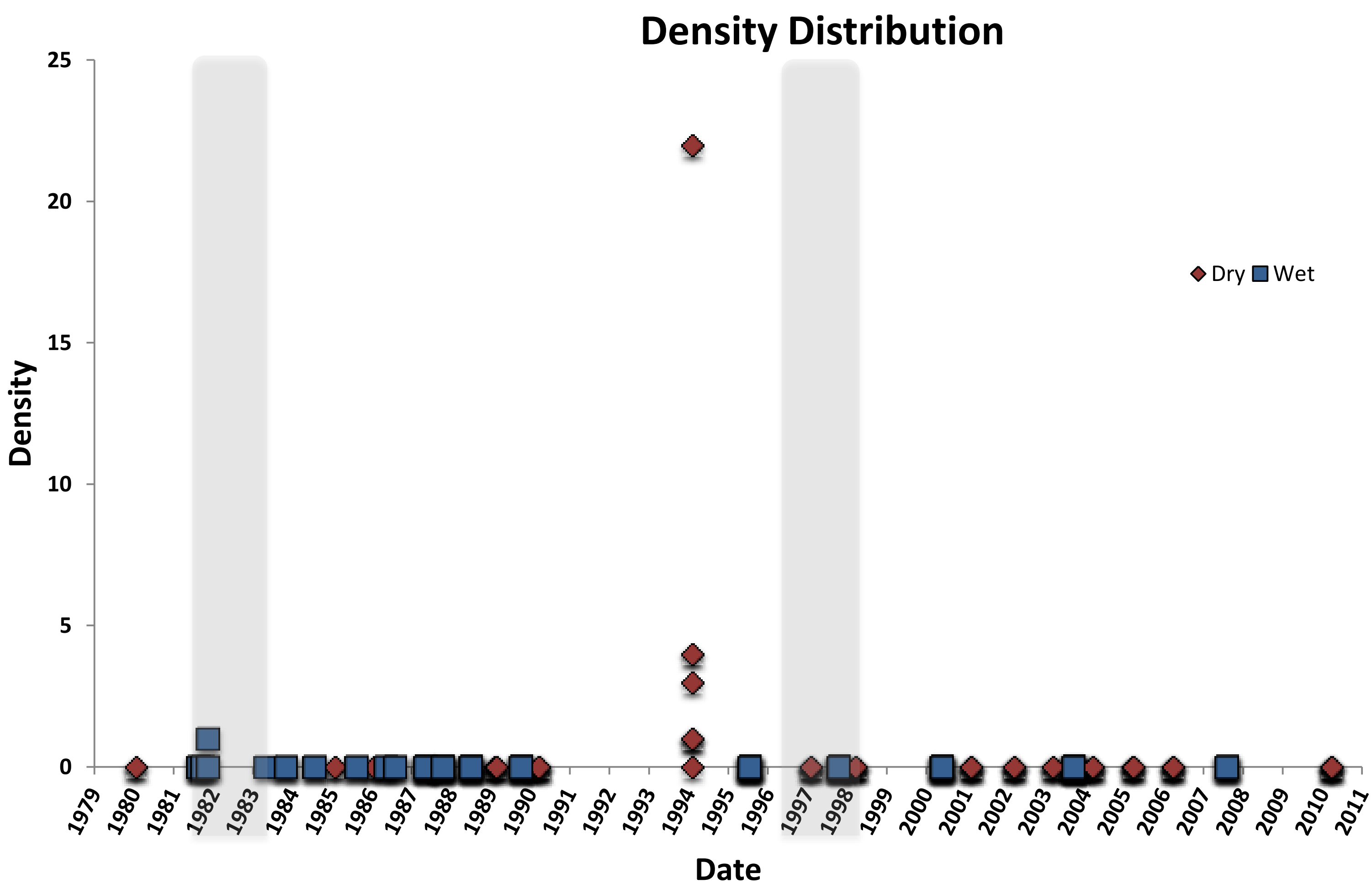
Lutjanus spp.

Snapper

Max. size: varies

Trophic group: Carnivore



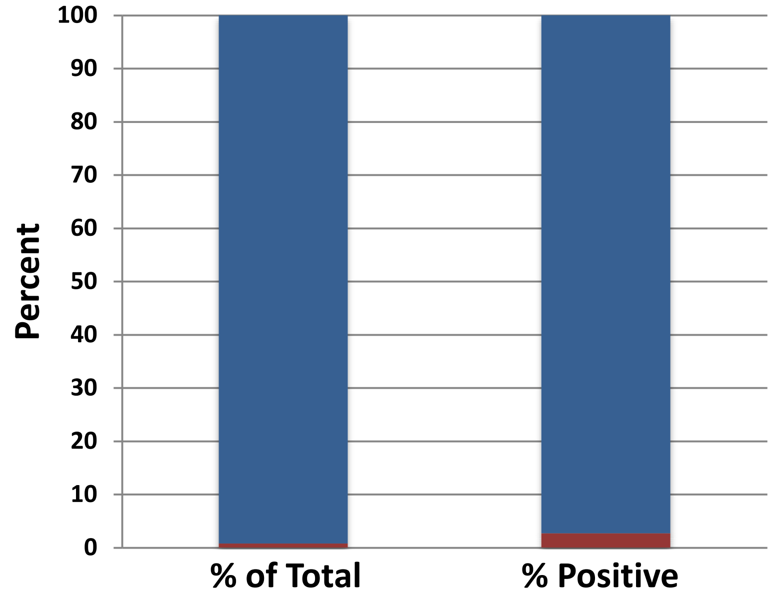


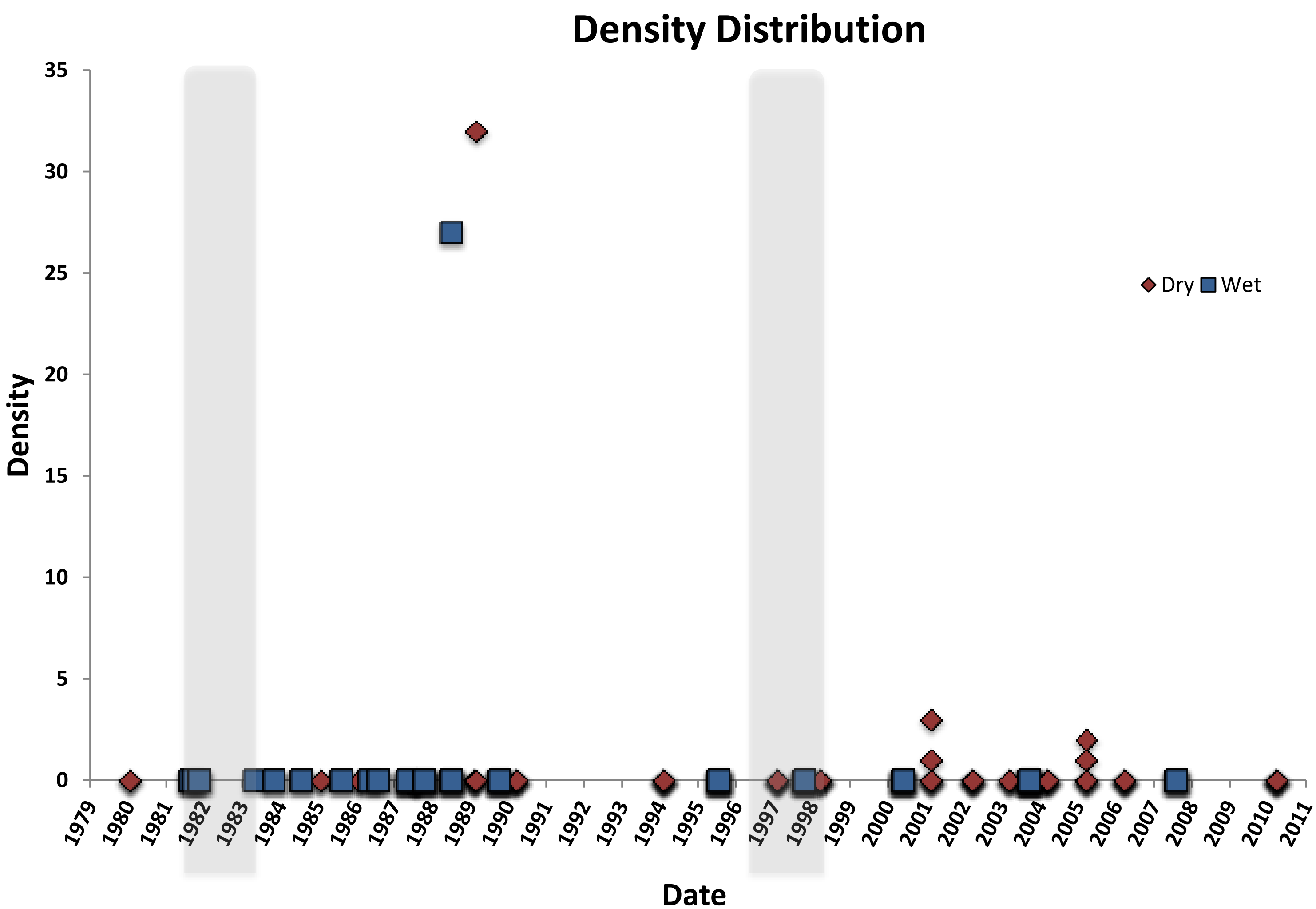
Mulloidichthys dentatus

Mexican goatfish

Max. size: 38 cm

Trophic group: Carnivore



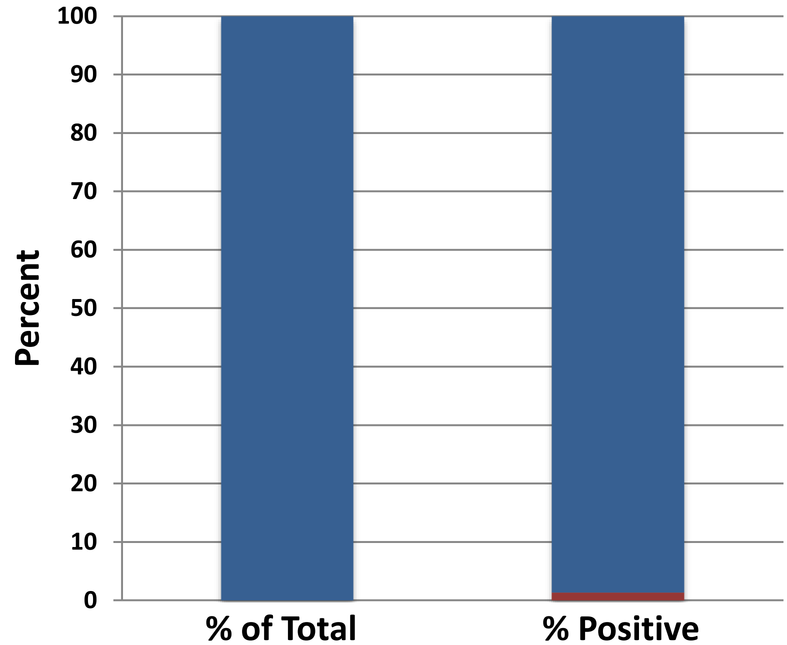


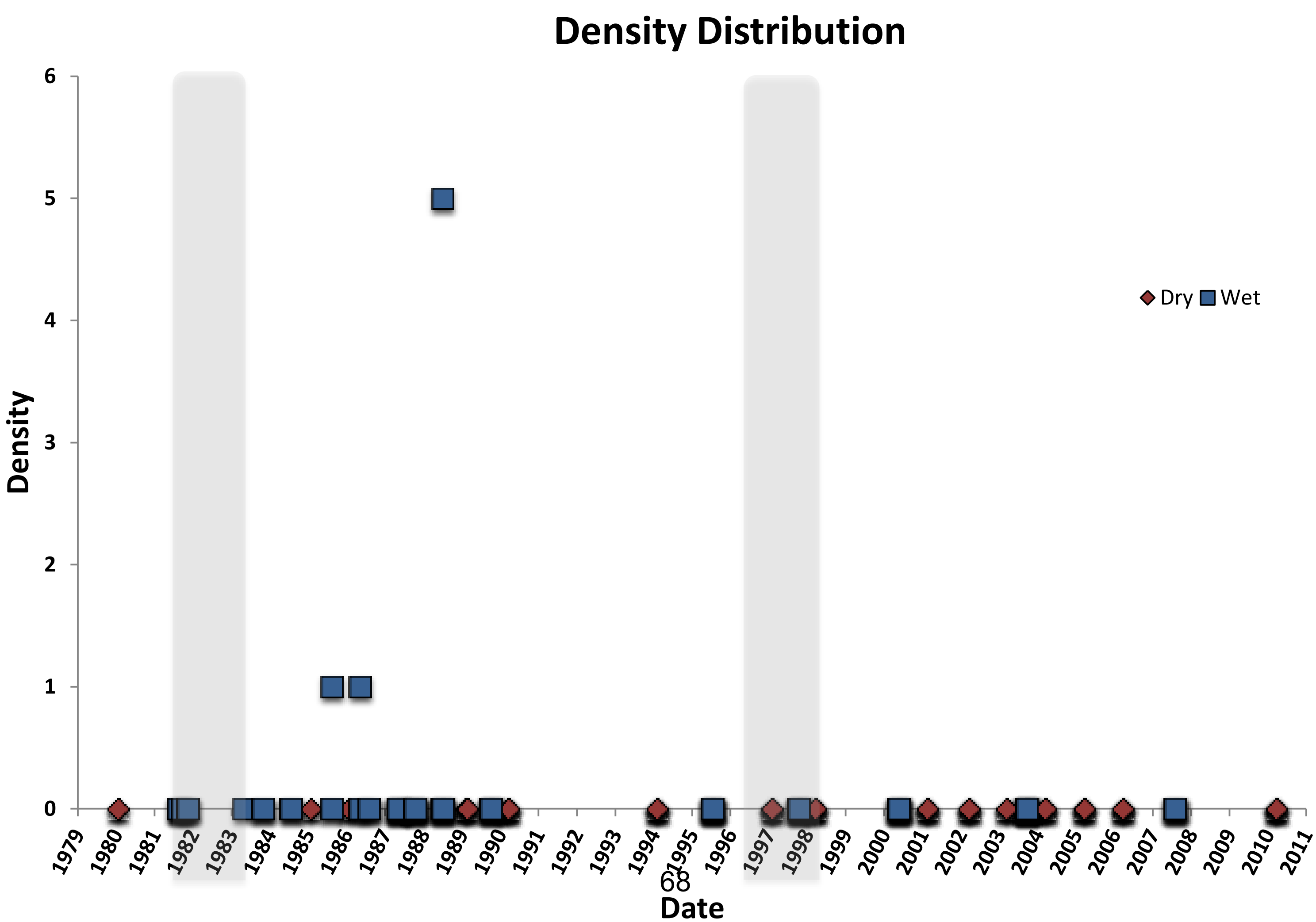
Myripristis leiognathus

Panamic soldierfish

Max. size: 18 cm

Trophic group: Planktivore



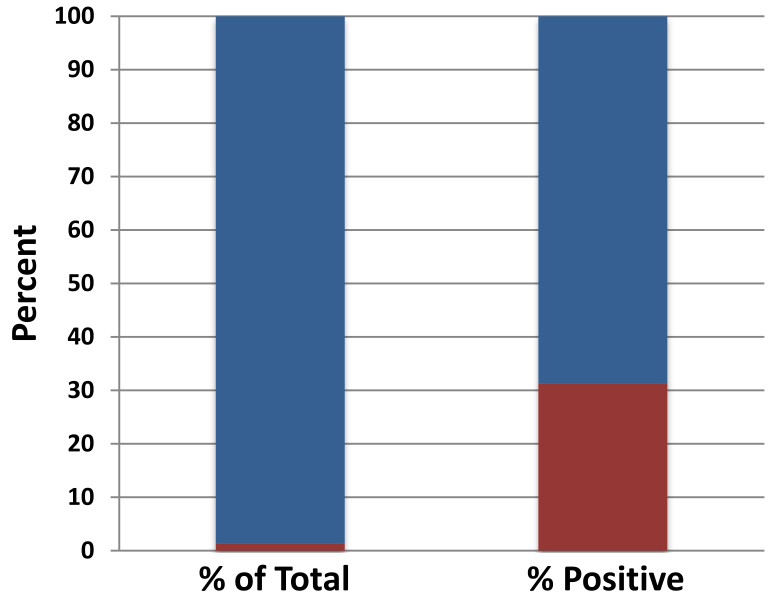


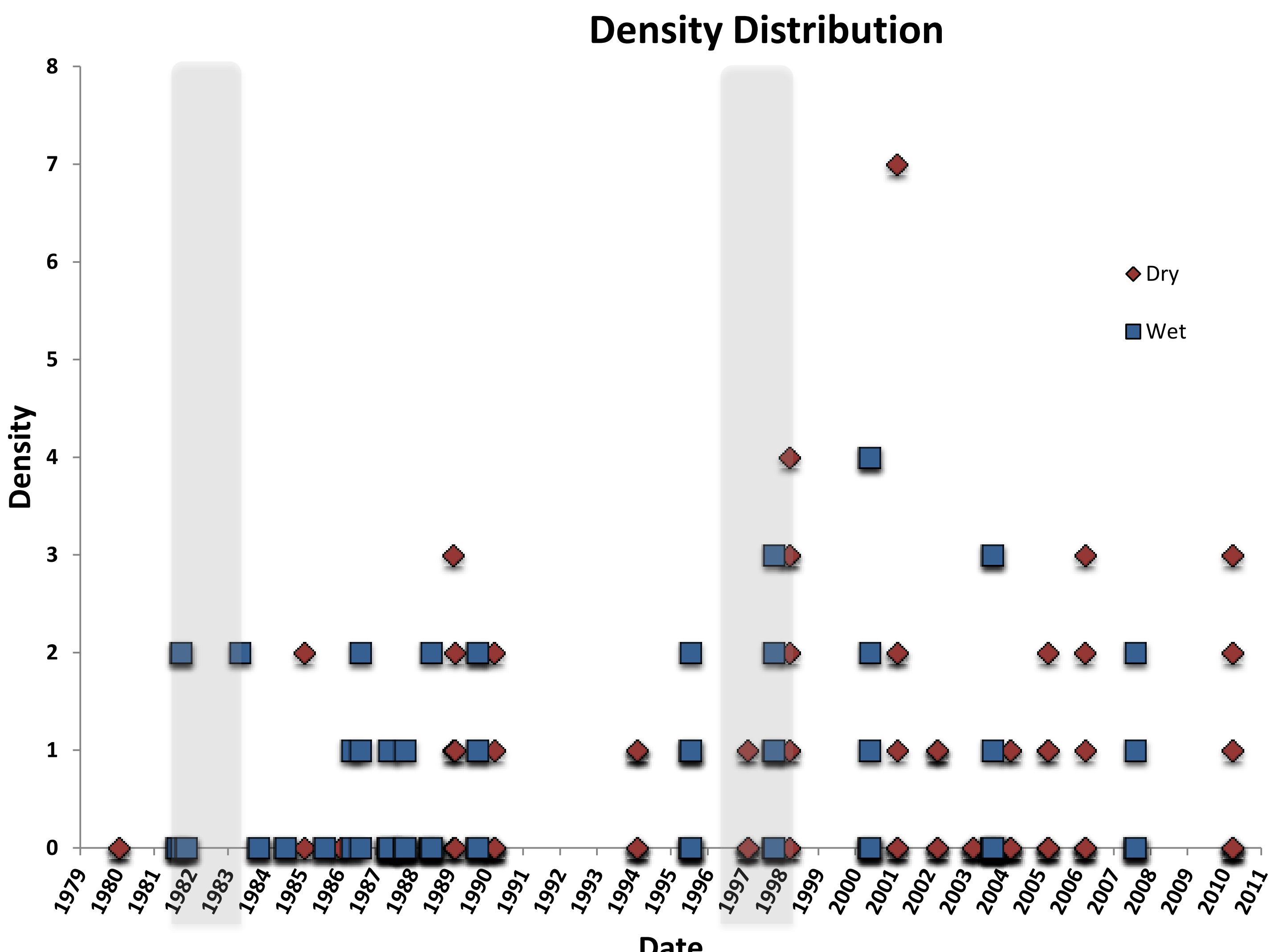
Novaculichthys taeniourus

Rock-mover wrasse

Max. size: 30 cm

Trophic group: Invertivore



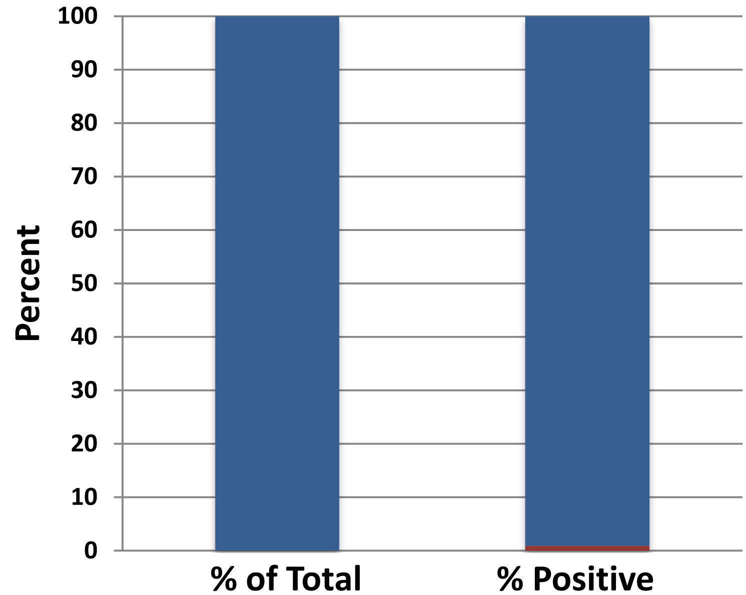


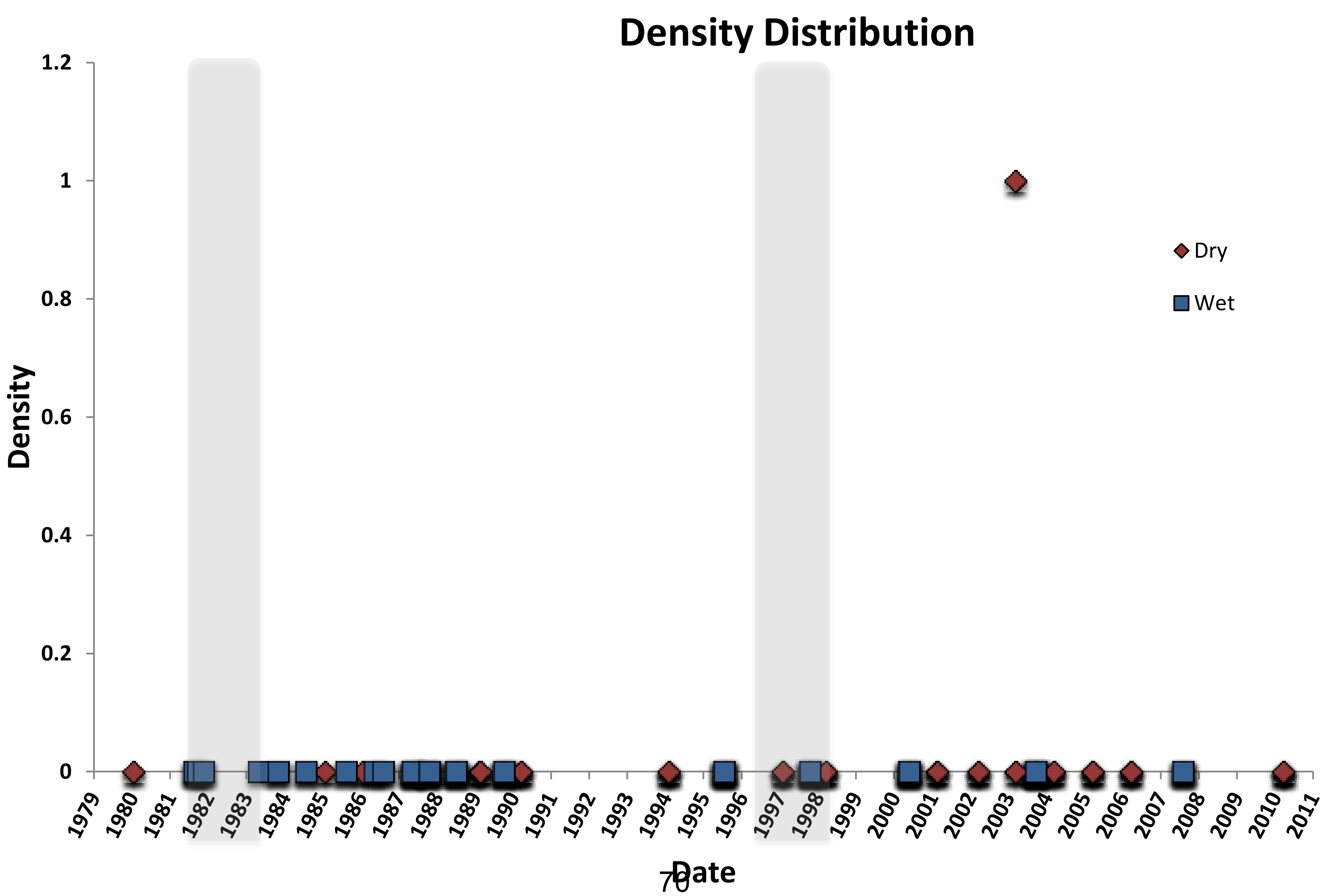
Ostracion meleagris

Spotted boxfish

Max. size: 25 cm

Trophic group: Invertivore



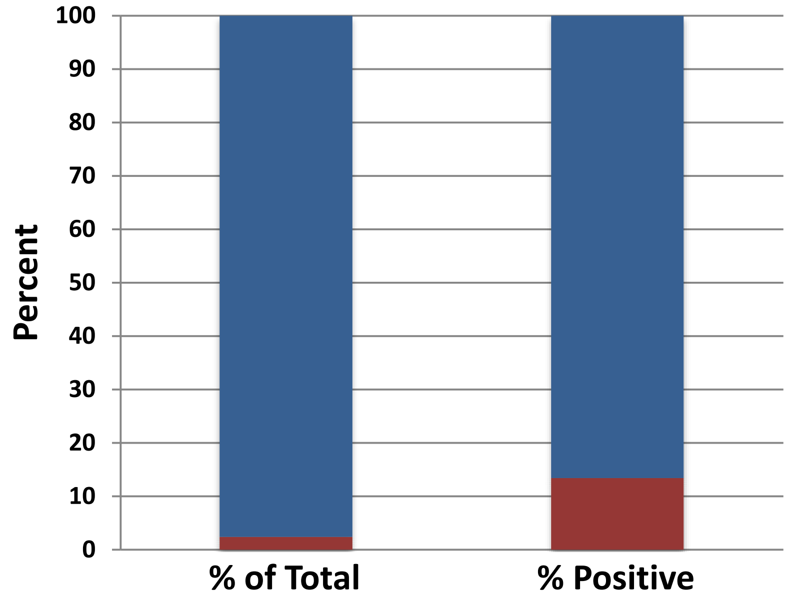


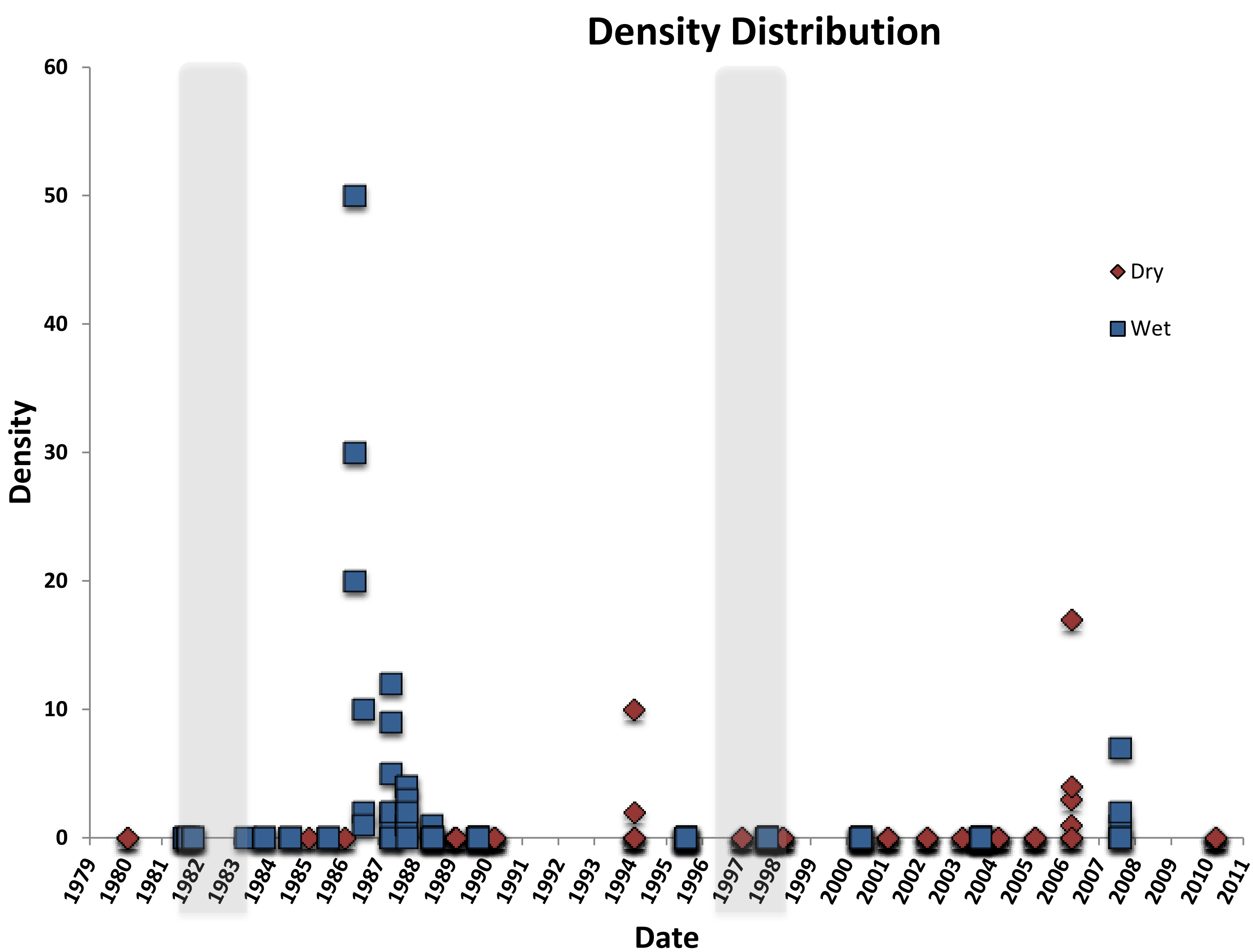
Paranthias colonus

Pacific creolefish

Max. size: 36 cm

Trophic group: Planktivore



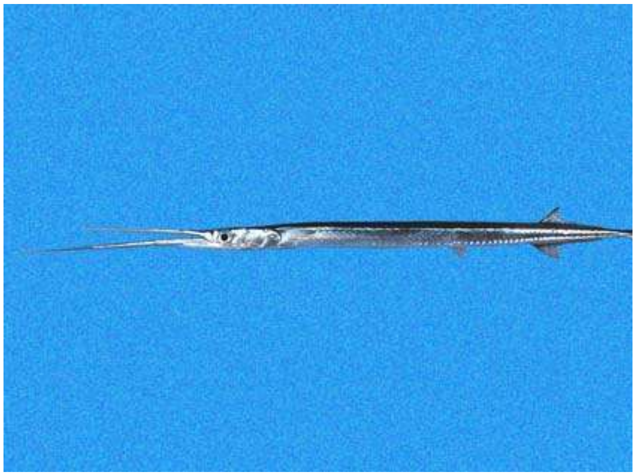


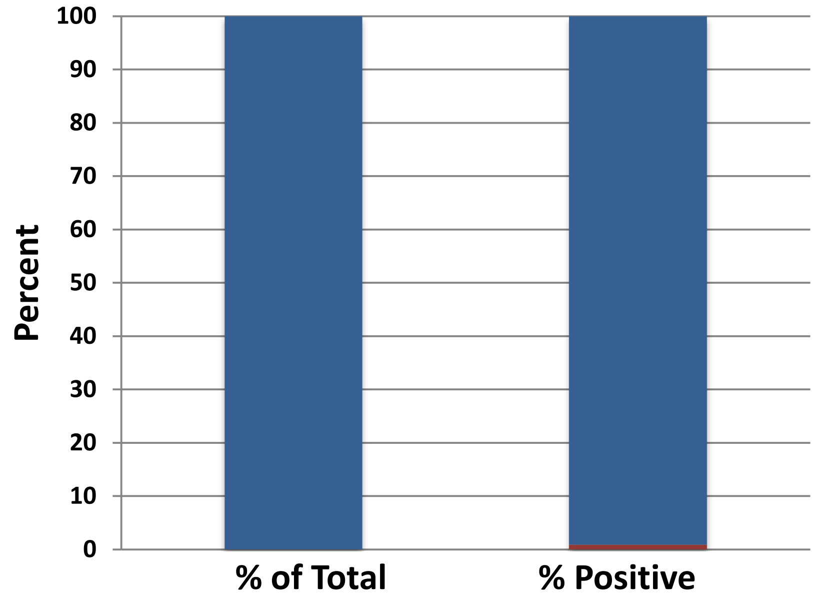
Platybelone argalus

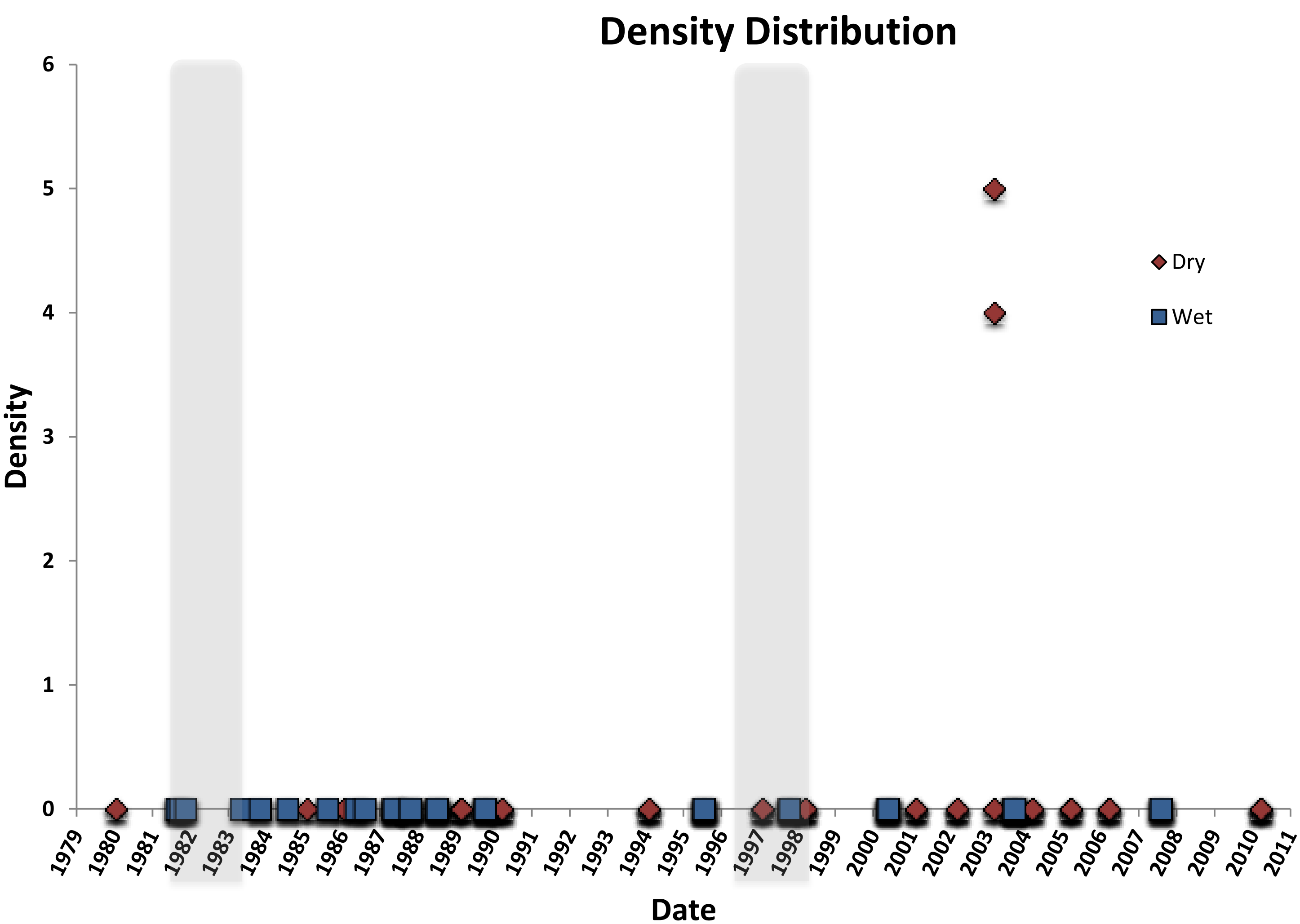
Baja keeltail needlefish

Max. size: 50 cm

Trophic group: Carnivore





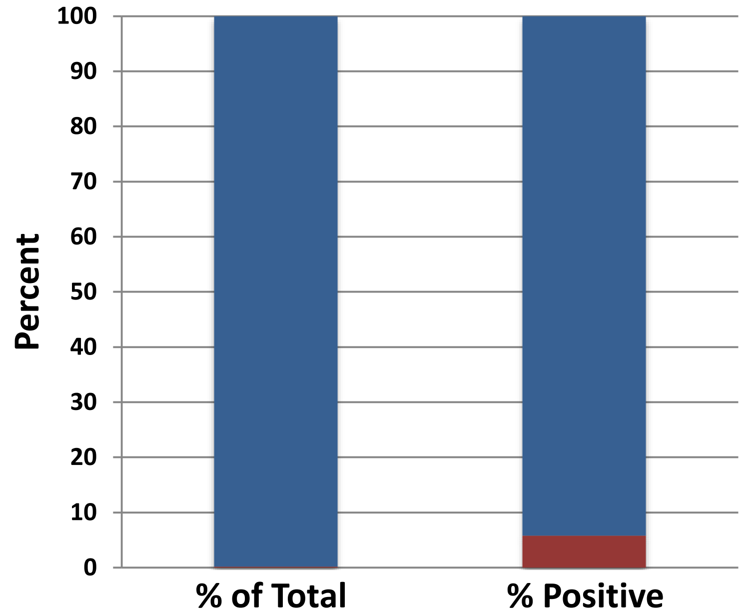


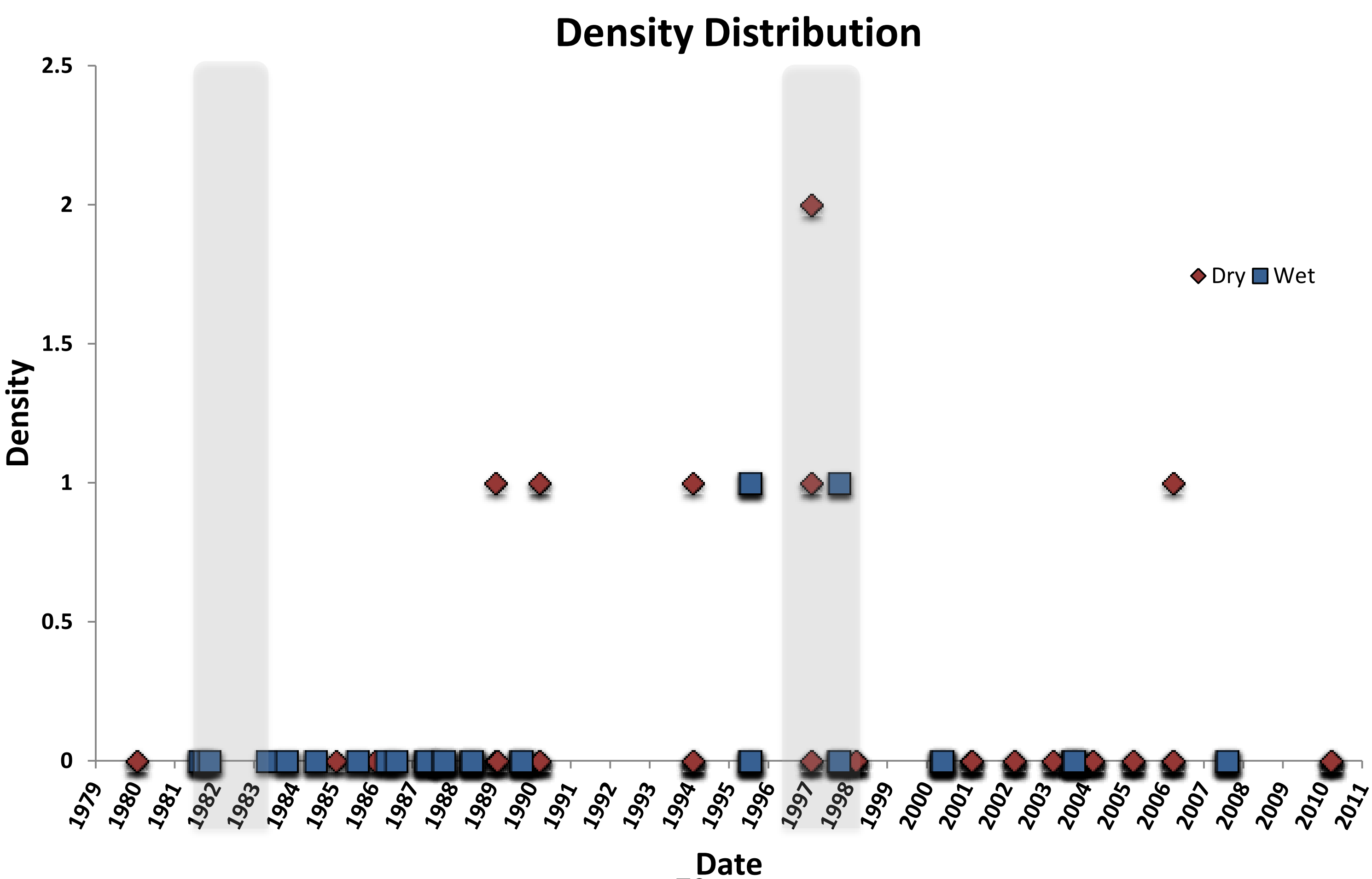
Pomacanthus zonipectus

Cortez angelfish

Max. size: 50 cm

Trophic group: Omnivore (Herbivore, Invertivore, Corallivore, Cleaner)



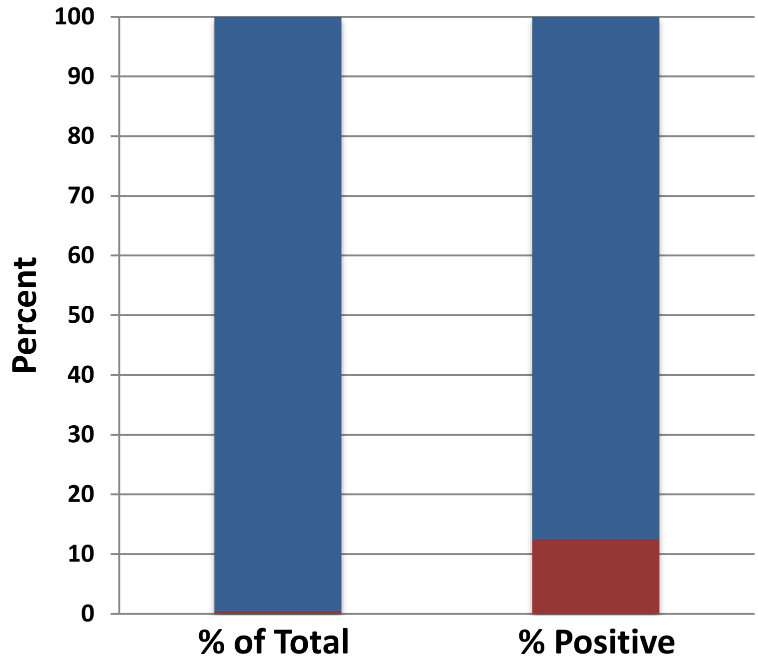


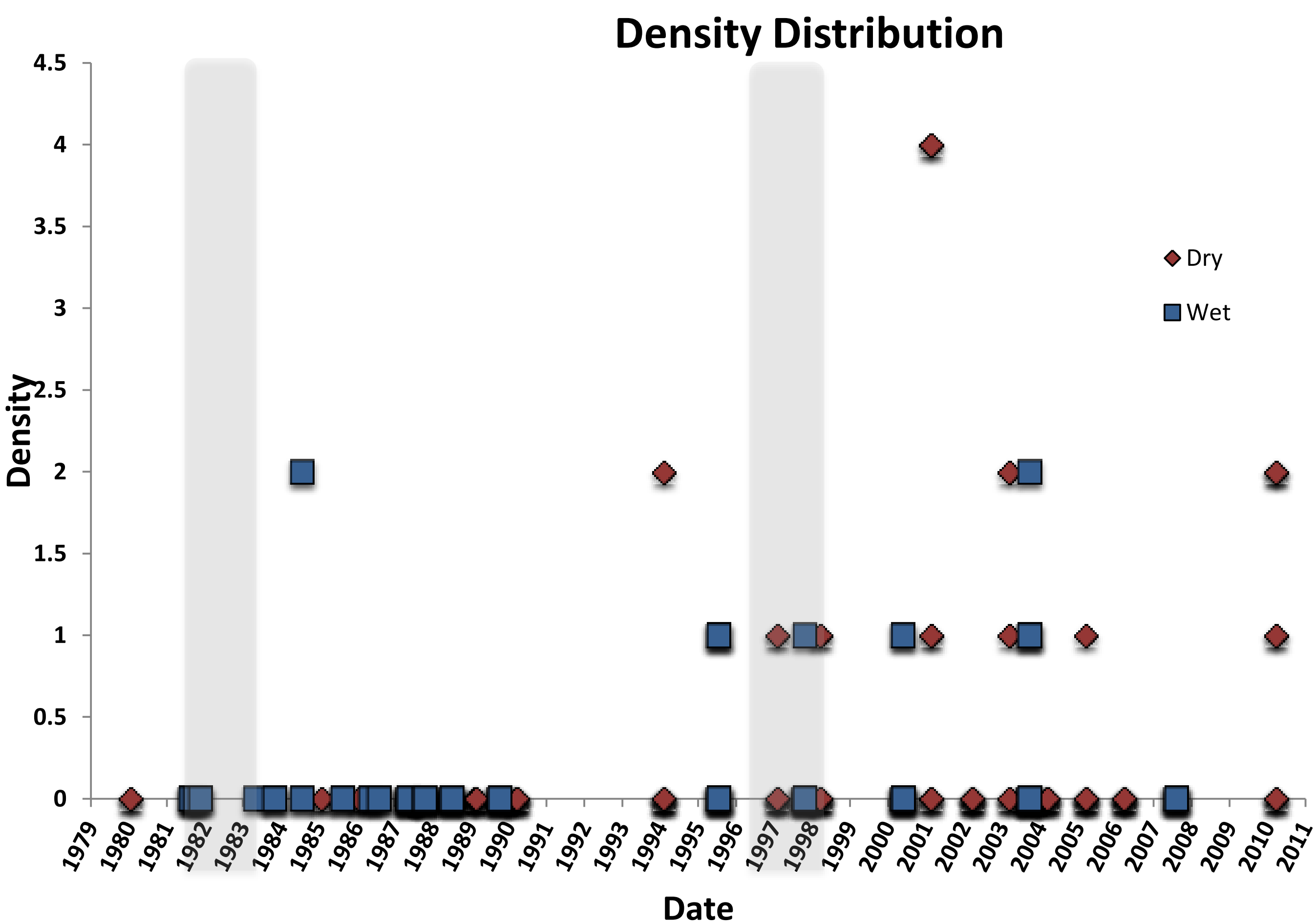
Pseudobalistes naufragium

Blunthead triggerfish

Max. size: 100 cm

Trophic group: Invertivore



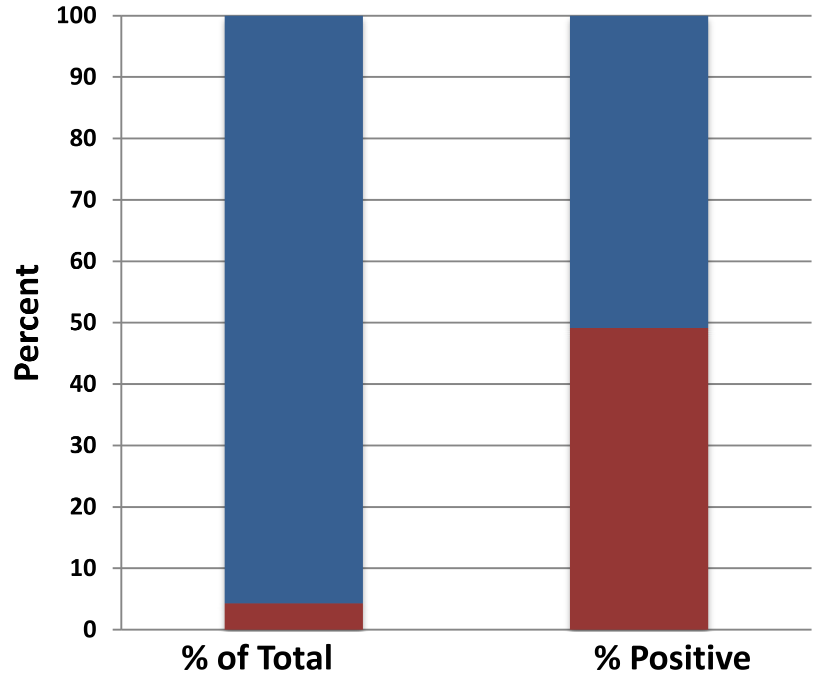


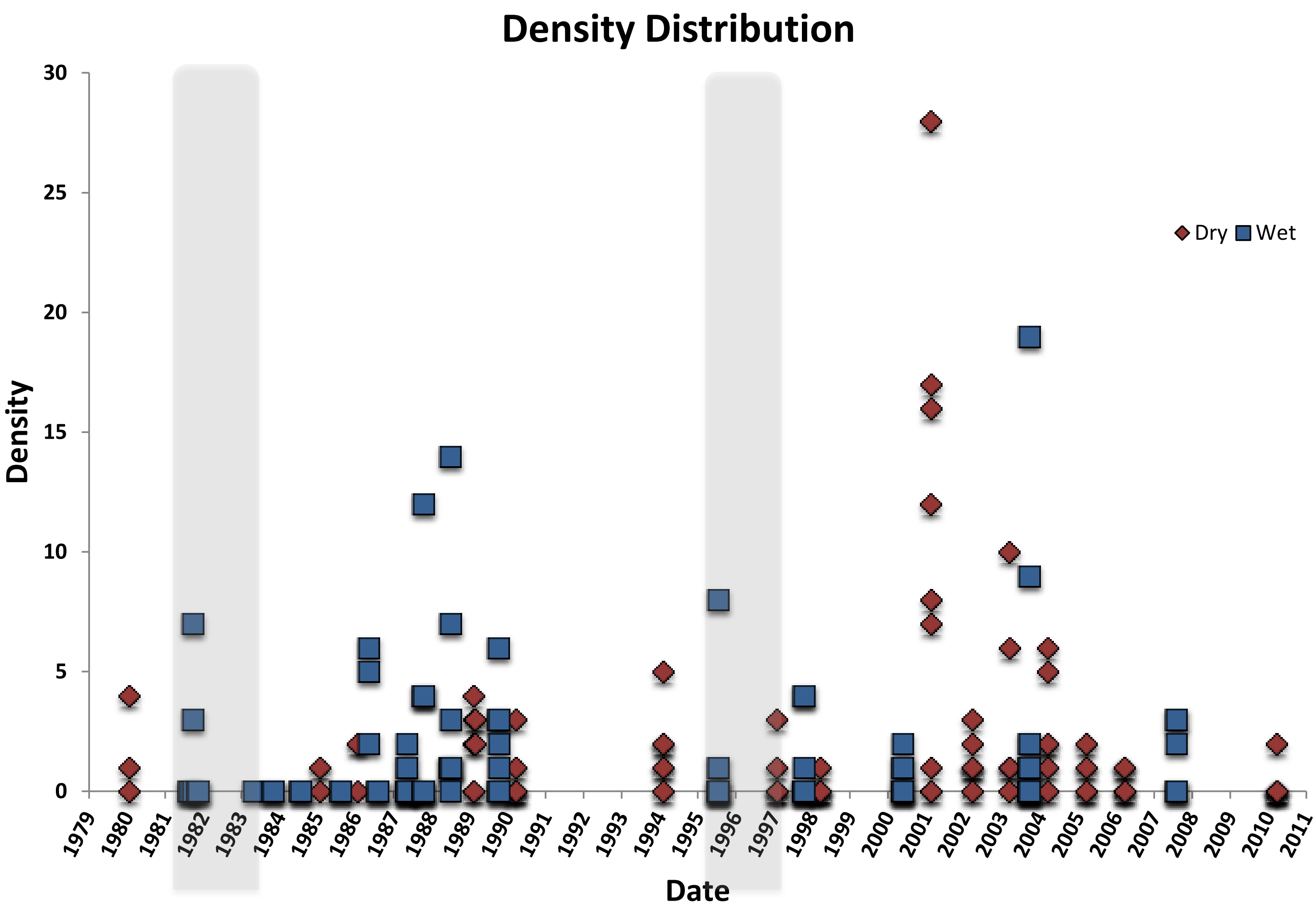
Scarus ghobban

Bluebarred parrotfish

Max. size: 90 cm

Trophic group: Herbivore



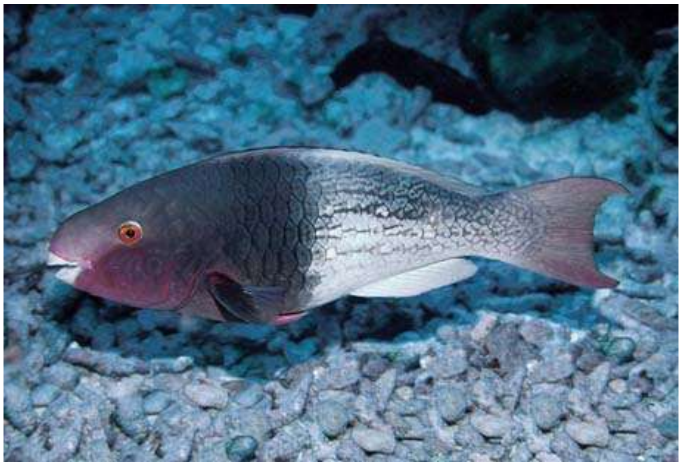


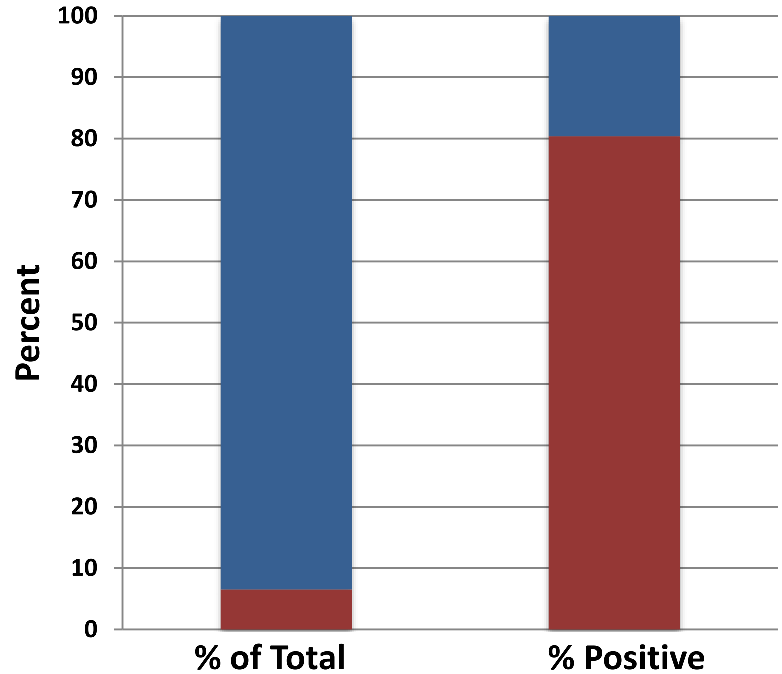
Scarus rubroviolaceus

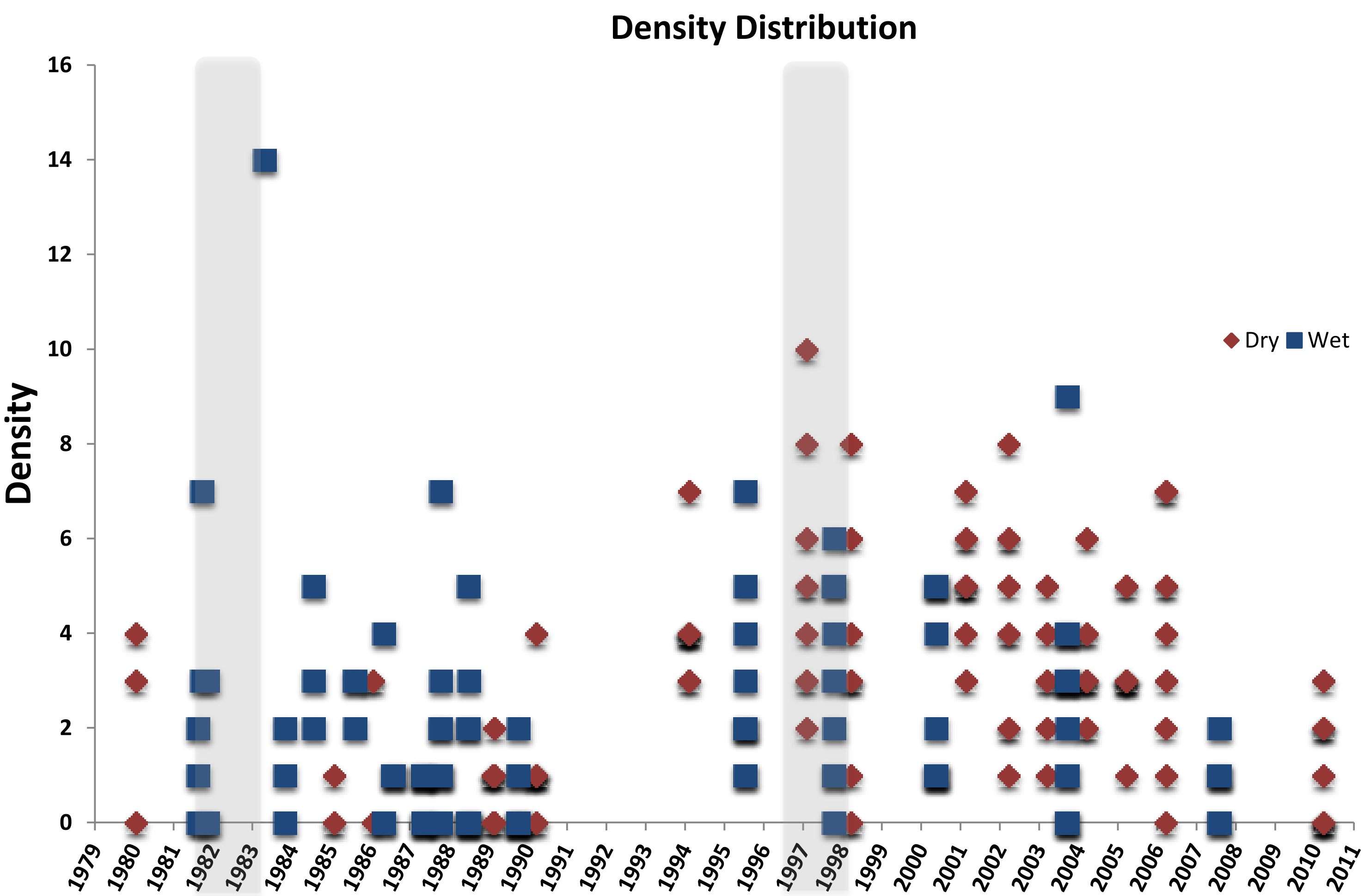
Bicolor parrotfish

Max. size: 71 cm

Trophic group: Herbivore





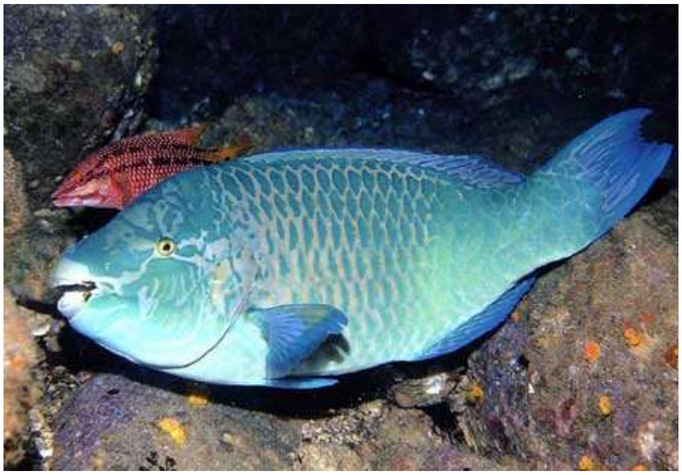


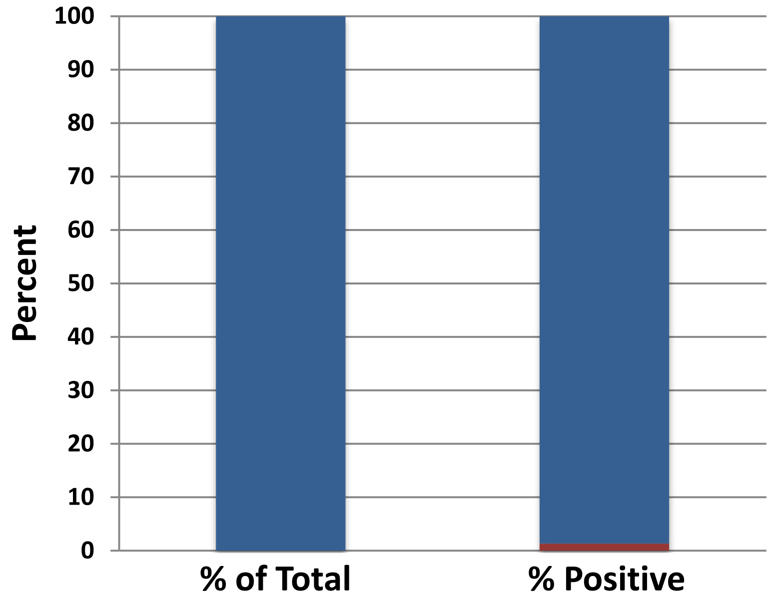
Scarus compressus

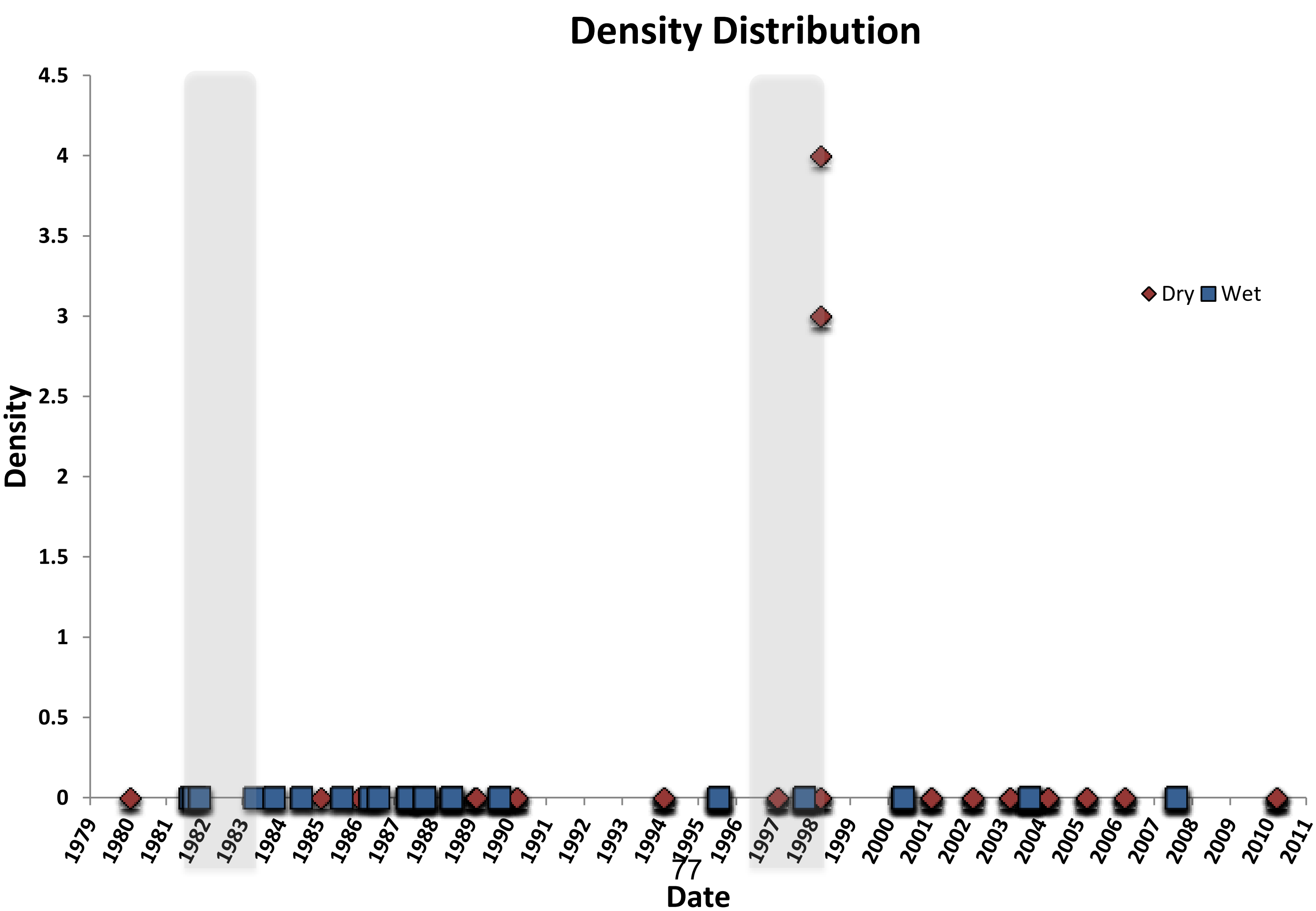
Azure parrotfish

Max. size: 60 cm

Trophic group: Herbivore





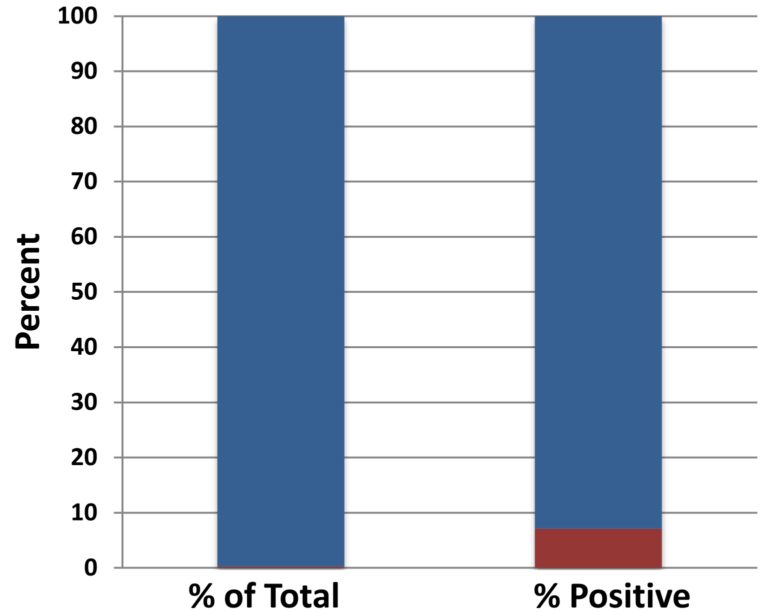


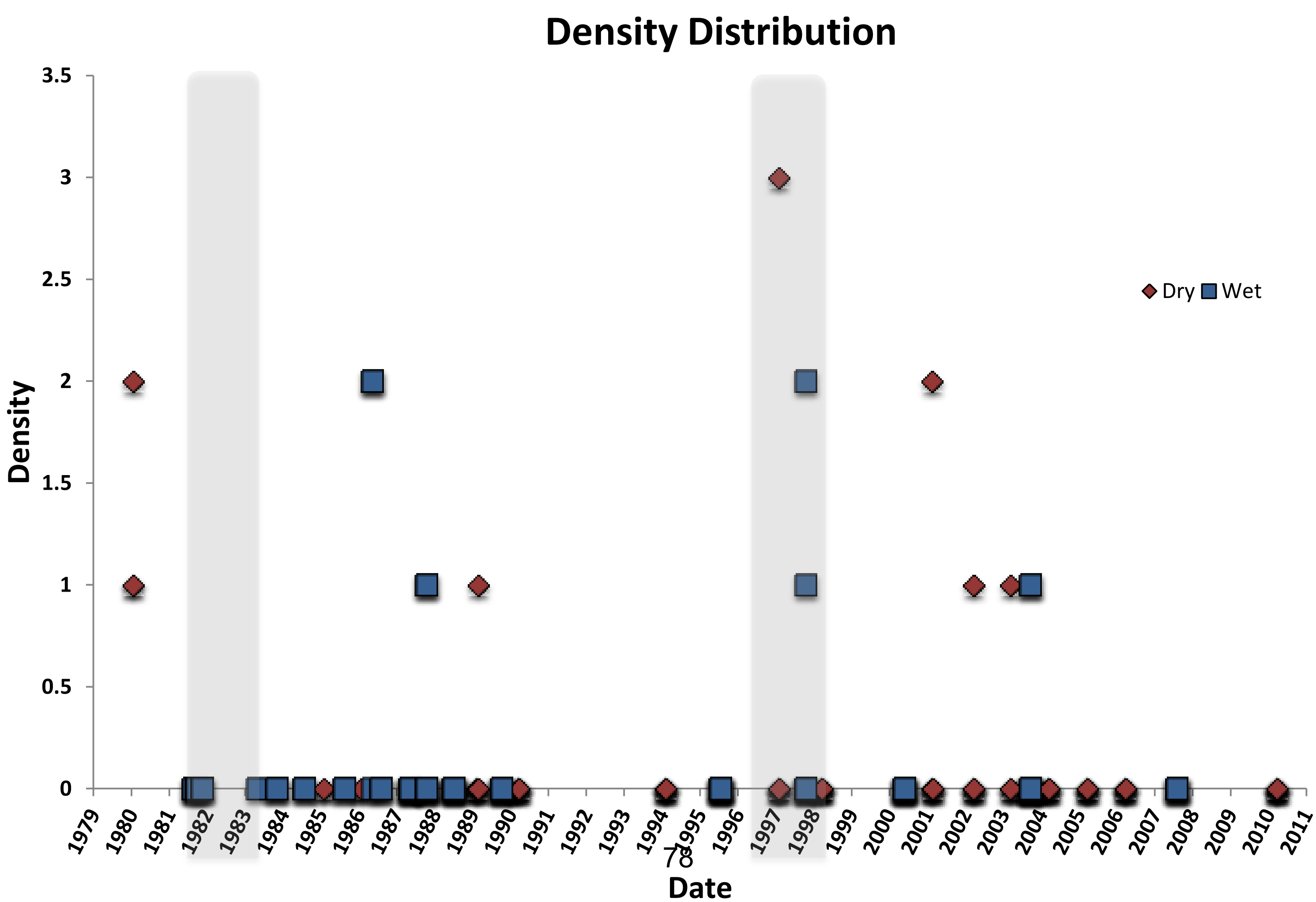
Scarus perrico

Bumphead parrotfish

Max. size: 80 cm

Trophic group: Herbivore



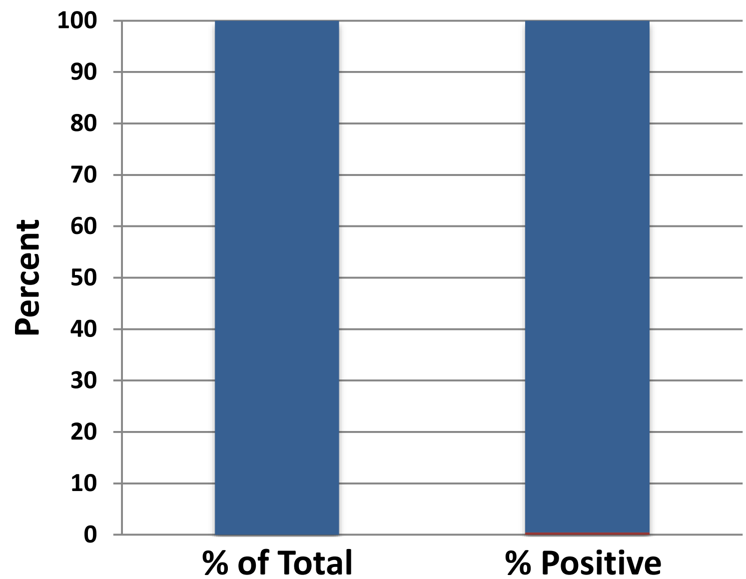


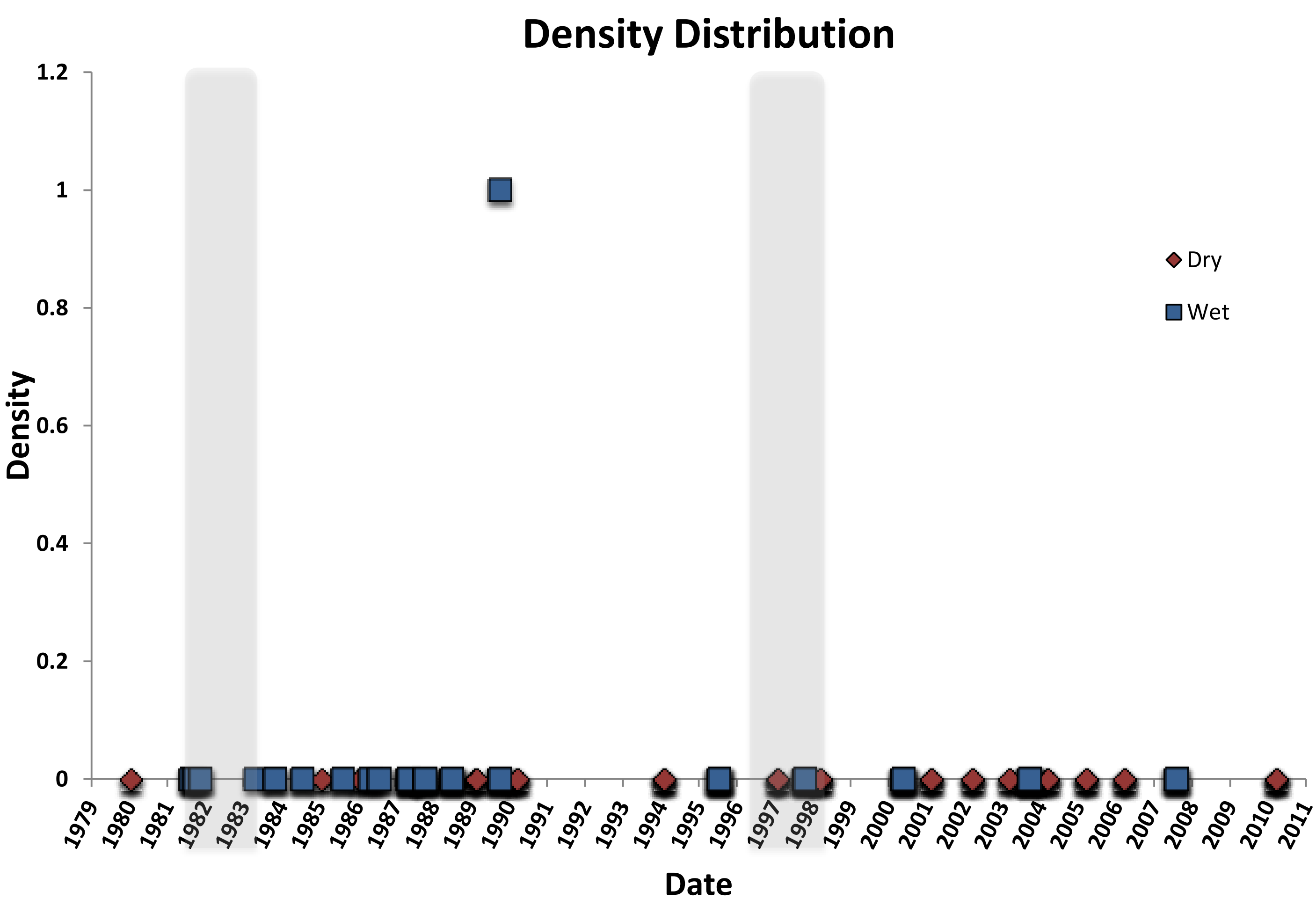
Scarus spp.

Parrotfish

Max. size: N/A

Trophic group: Herbivore



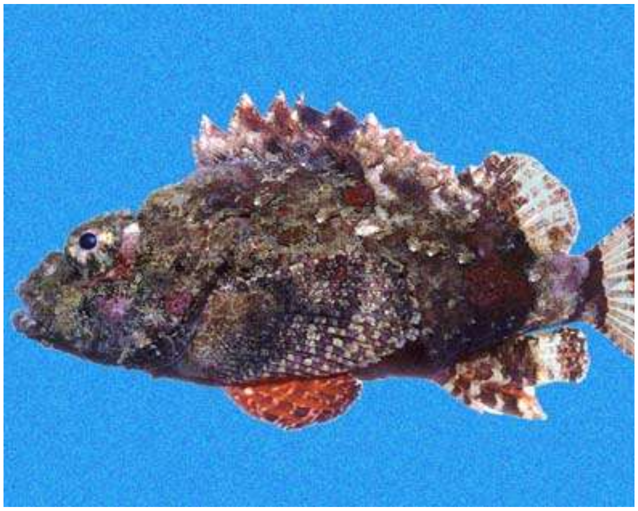


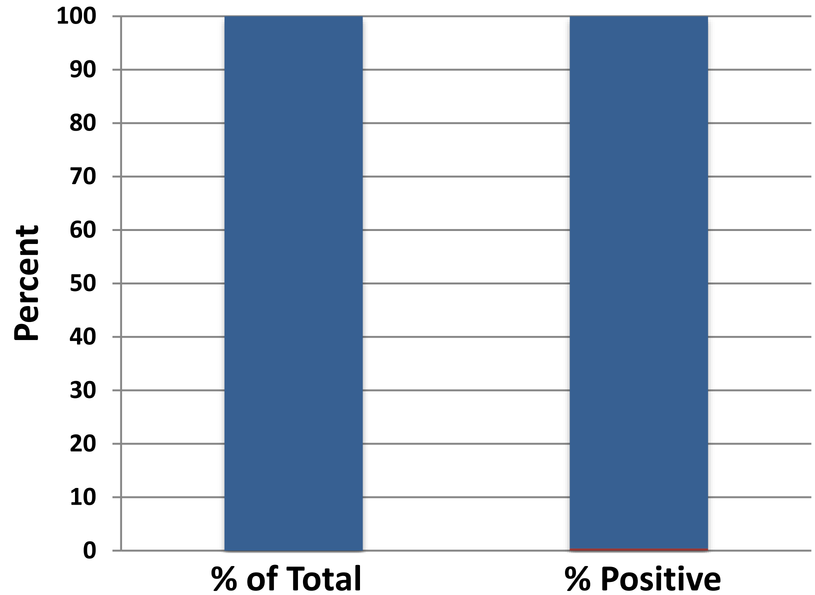
Scorpaena mystes

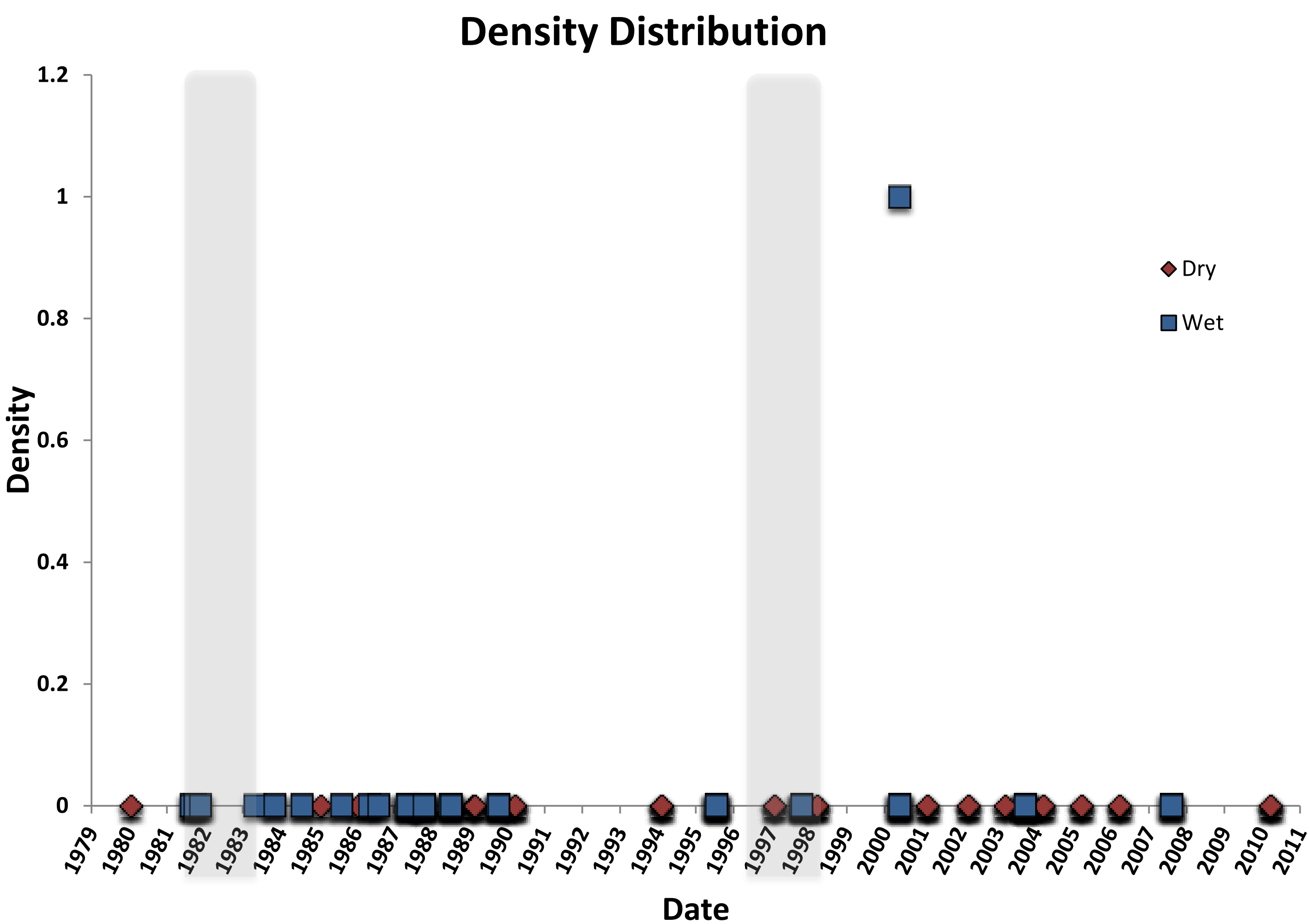
Pacific spotted scorpionfish

Max. size: 46 cm

Trophic group: Carnivore





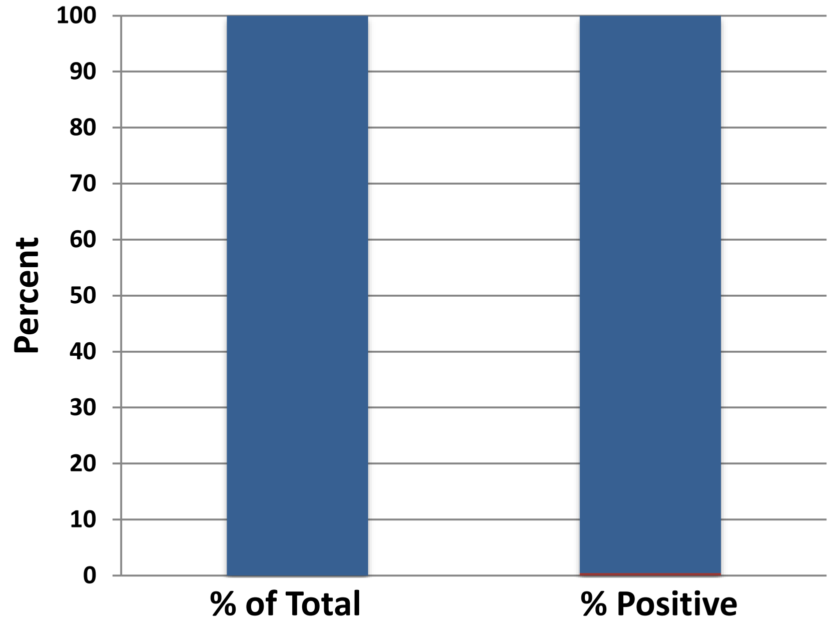


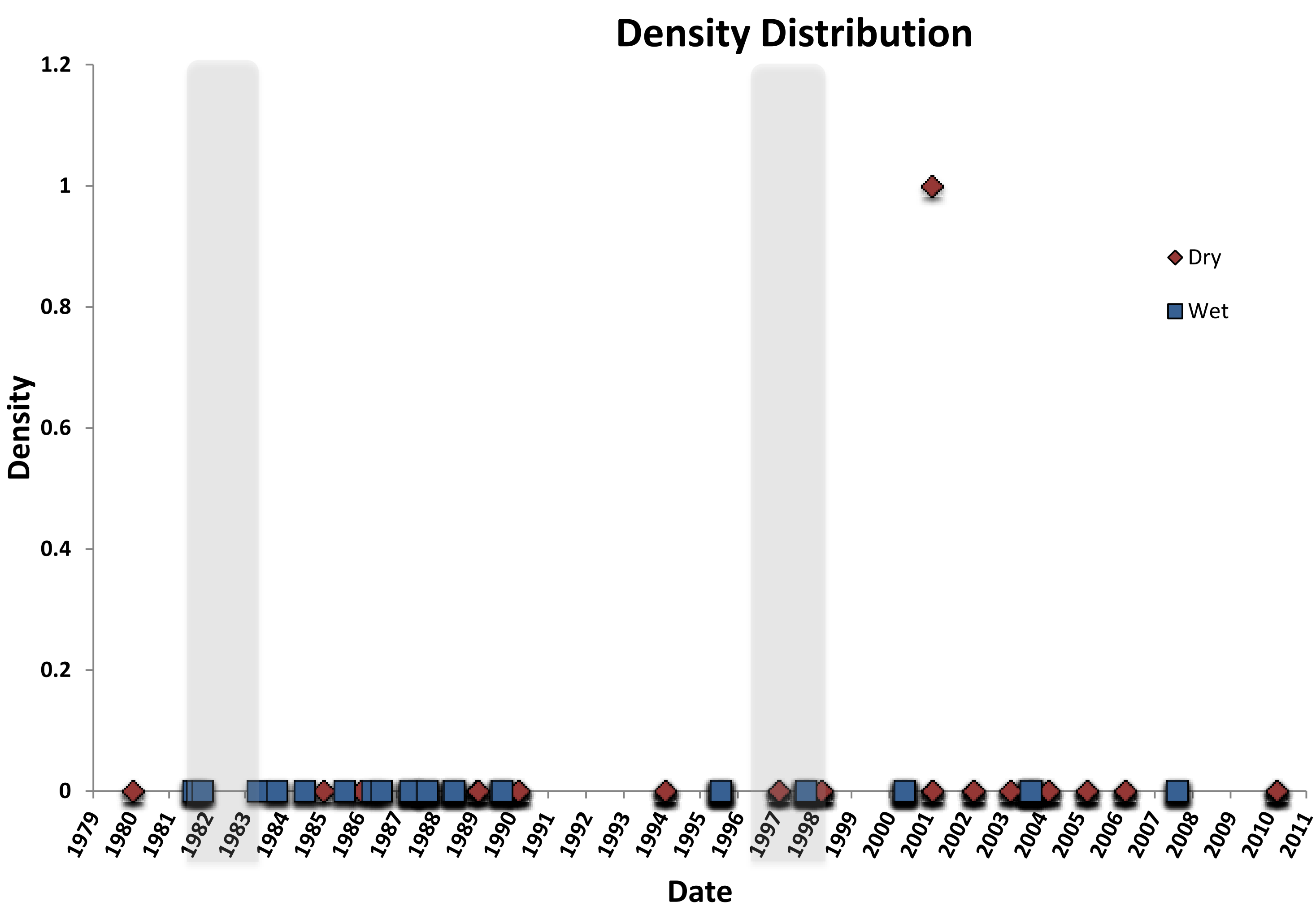
Sectator ocyurus

Bluestriped sea-chub

Max. size: 70 cm

Trophic group: Planktivore



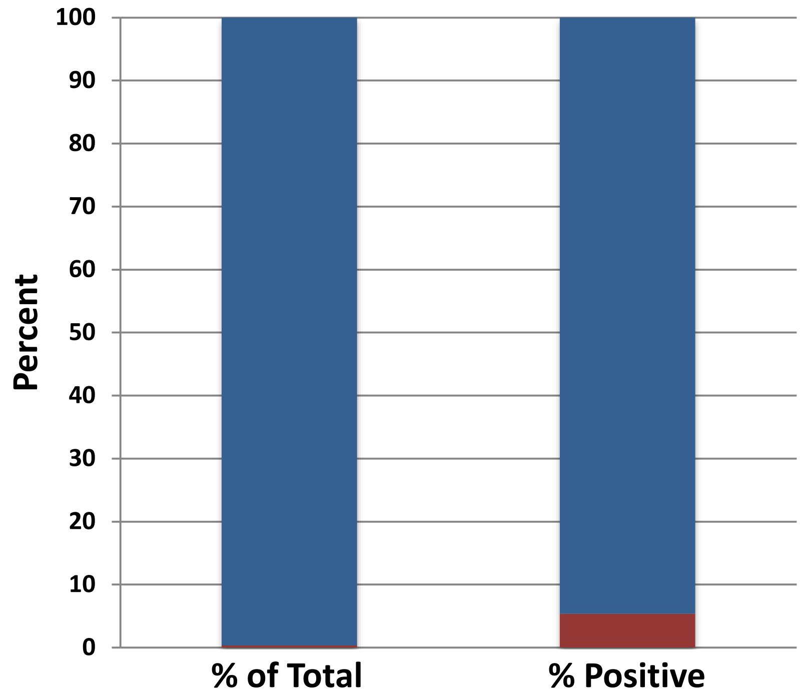


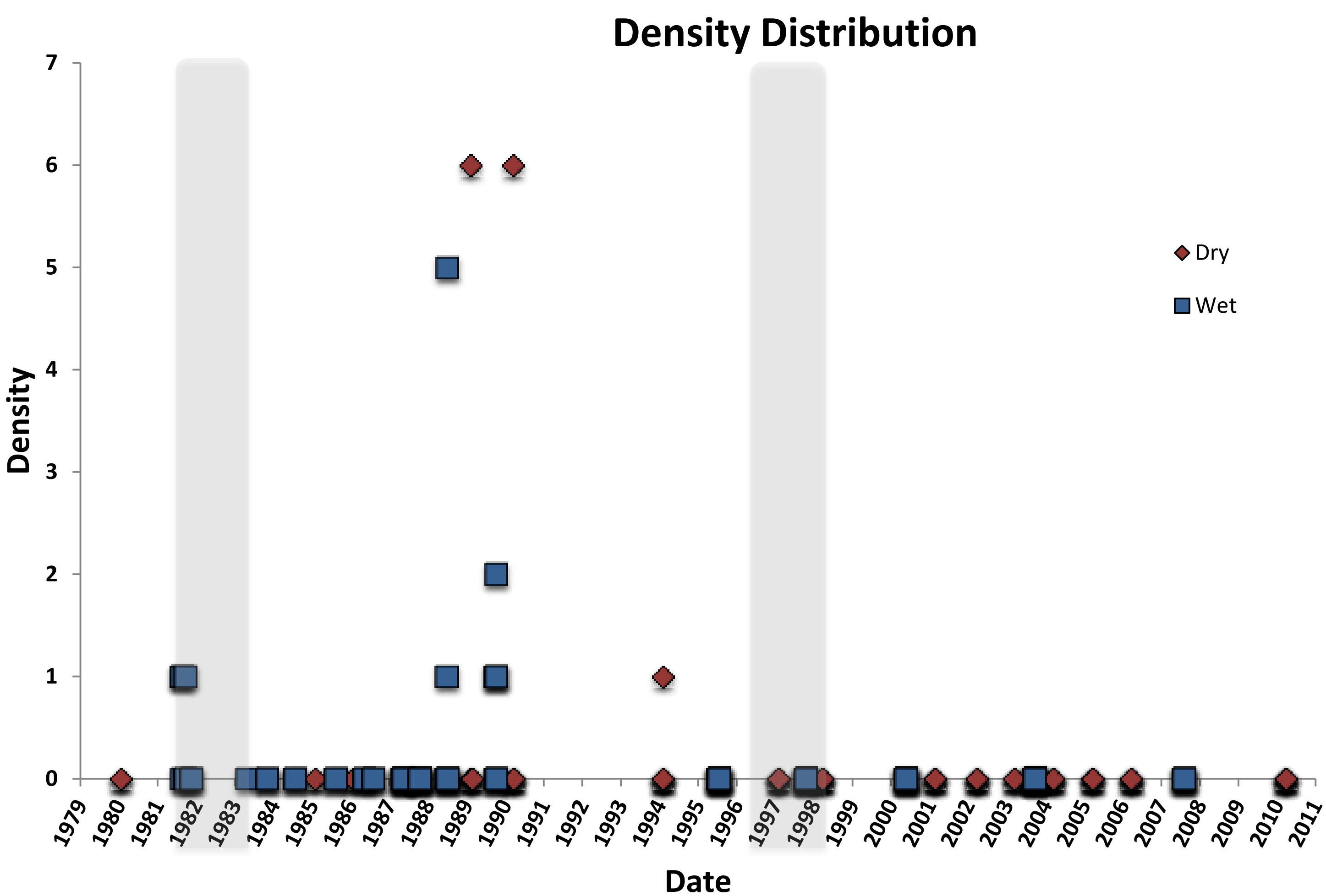
Seriola rivoliana

Pacific amberjack

Max. size: common up to 60 cm but can reach 157 cm

Trophic group: Carnivore



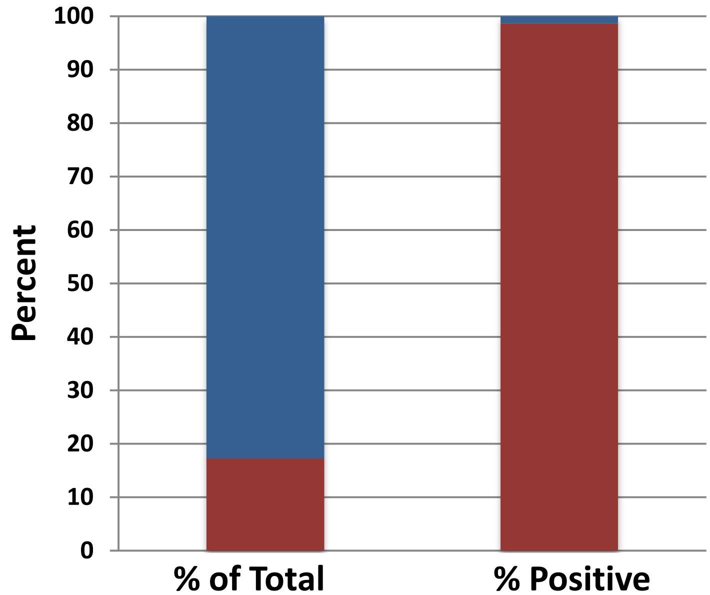


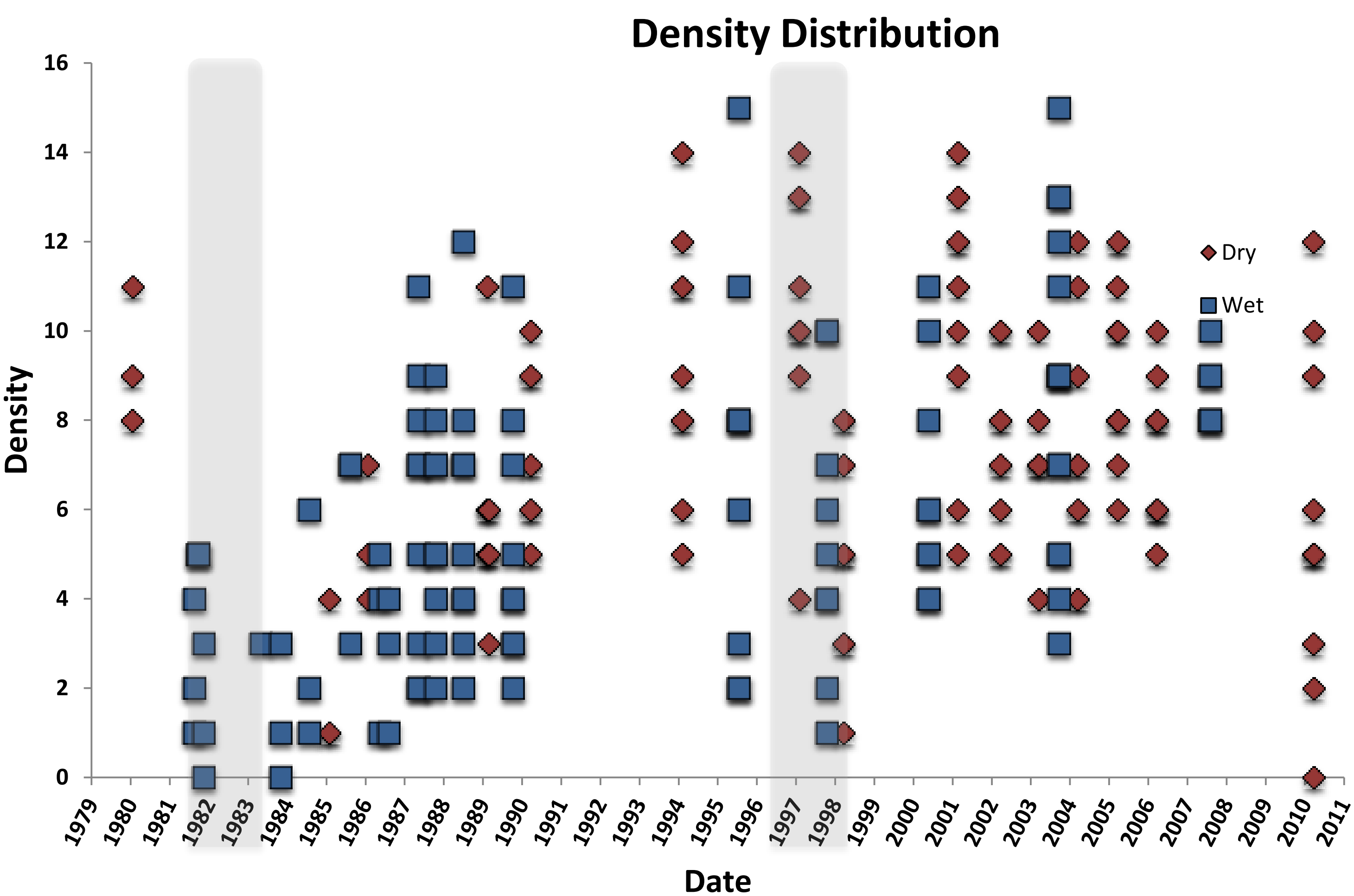
Sufflamen verres

Orange-side triggerfish

Max. size: 40 cm

Trophic group: Invertivore



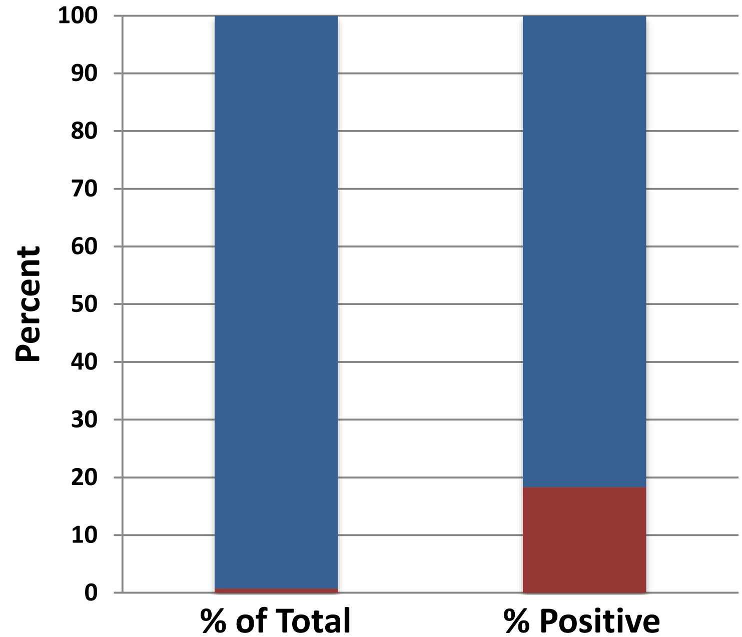


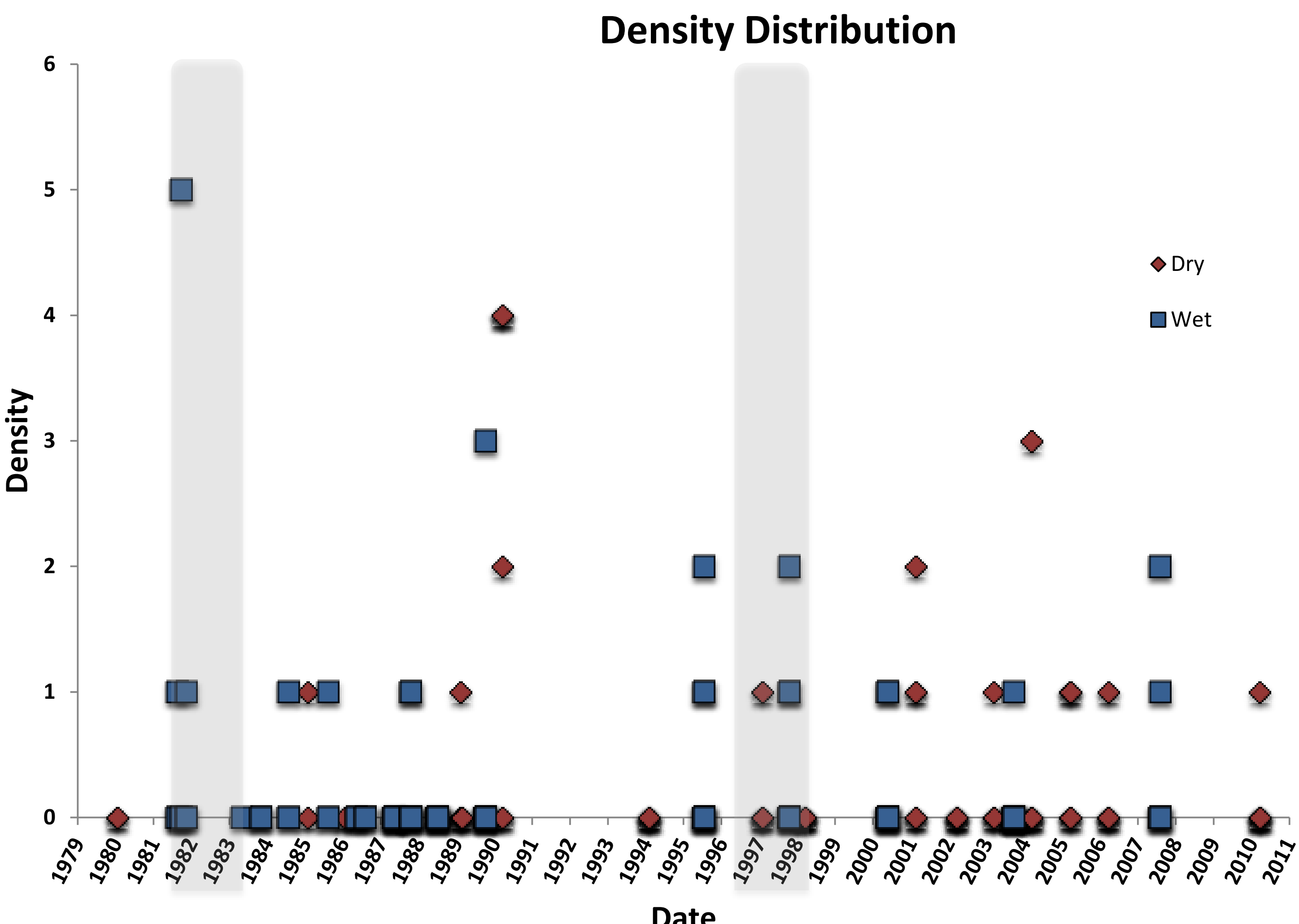
Thalassoma grammaticum

Green wrasse

Max. size: 32 cm

Trophic group: Invertivore



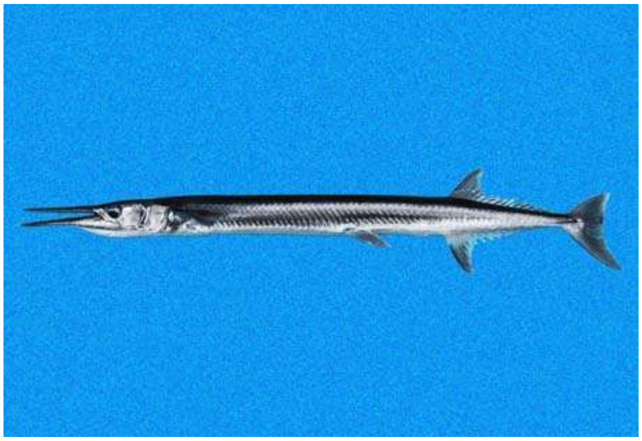


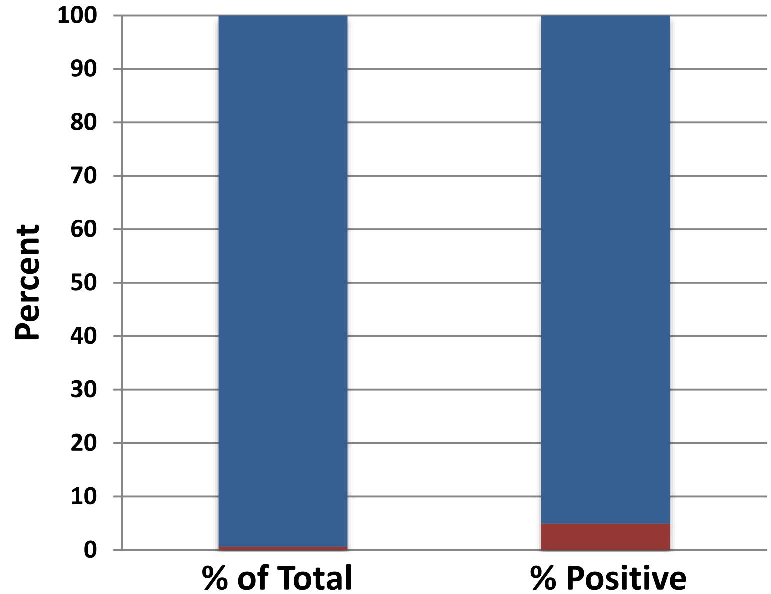
Tylosurus crocodilus fodiator

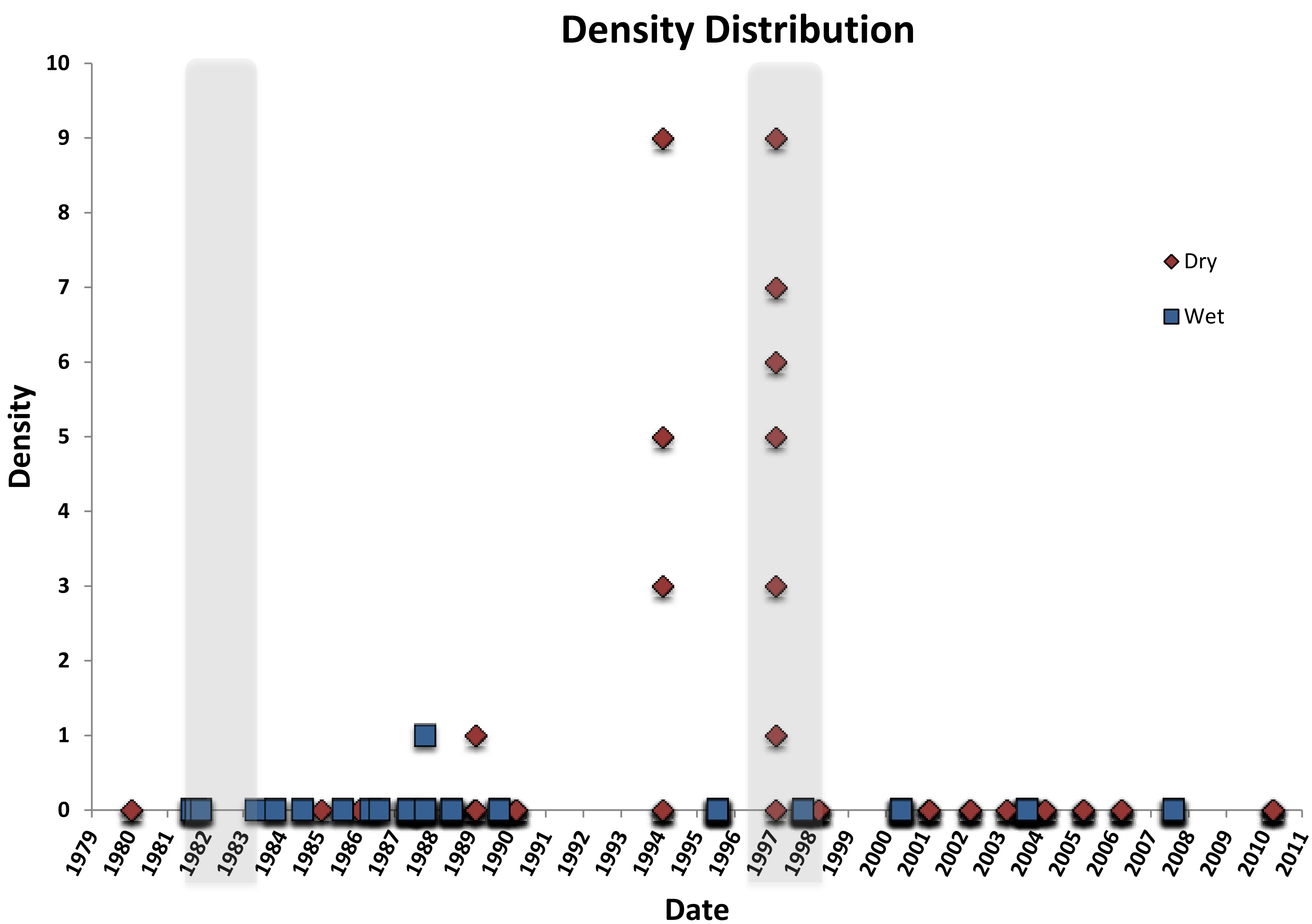
Crocodile needlefish

Max. size: 159 cm

Trophic group: Carnivore



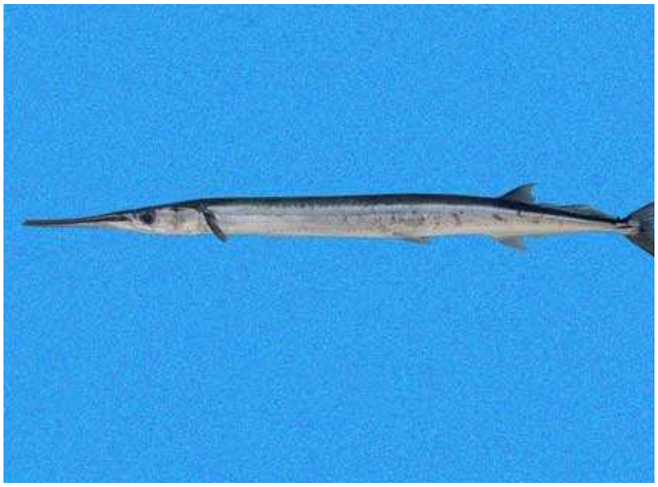


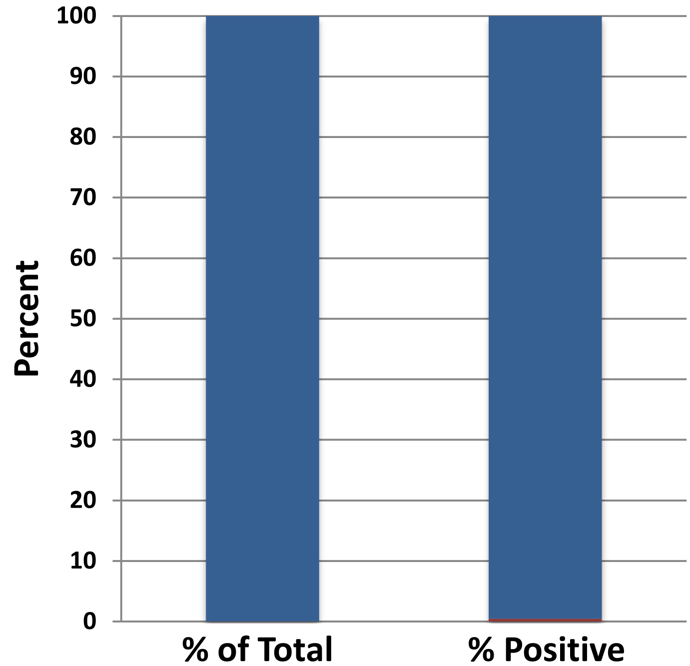


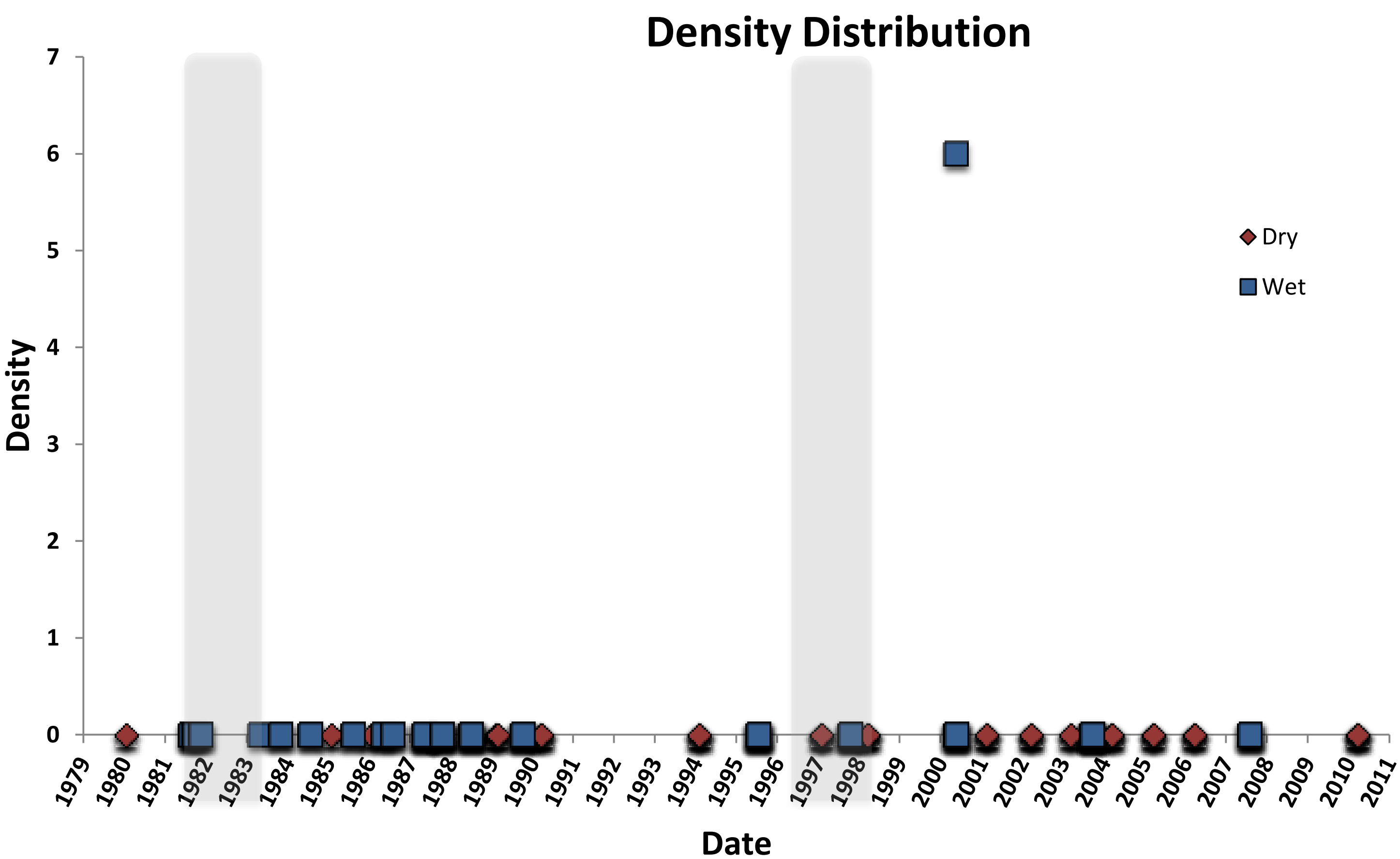
Tylosurus sp.

Max. size: N/A

Trophic group: Carnivore





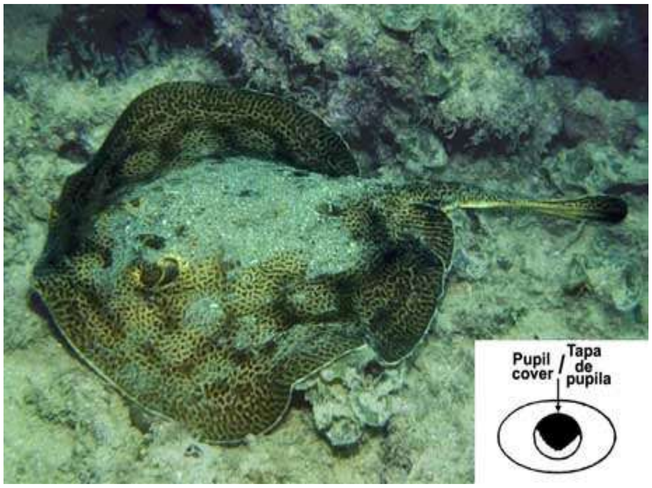


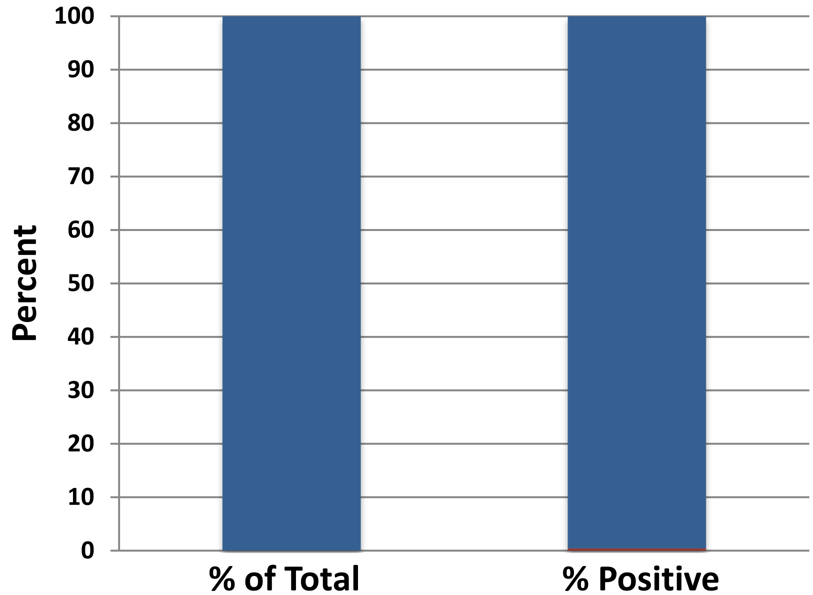
Urobatis halleri

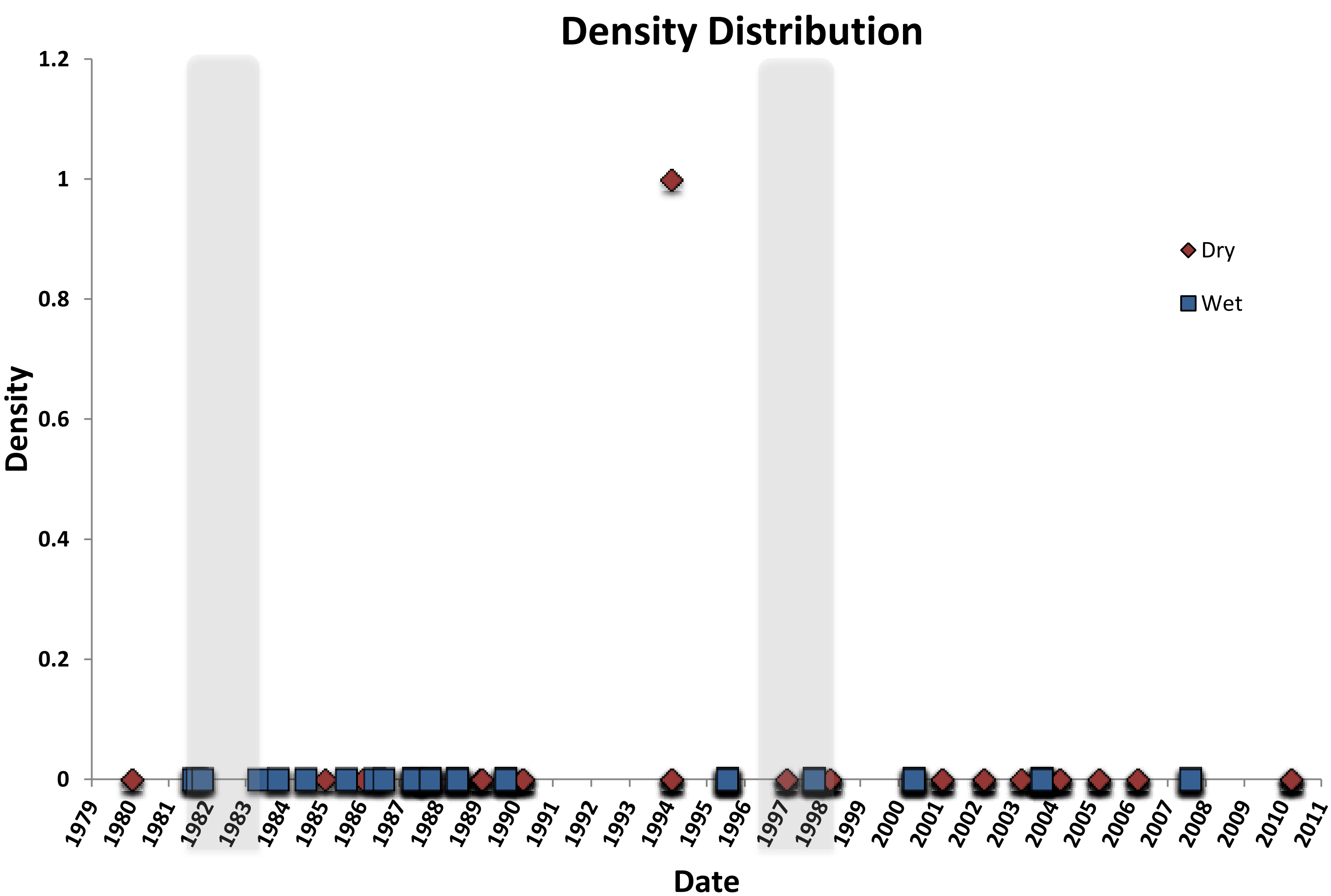
Hallers roundstingray

Max. size: 58 cm

Trophic group: Carnivore







Zanclus cornutus

Moorish idol

Max. size: 30 cm

Trophic group: Carnivore