

Depth Distribution Reveals Ontogenetic Movement Exhibited by  
Blue Rockfish (*Sebastes mystinus*)

By

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THESIS

Submitted in partial satisfaction of the degree requirements for the degree of

MASTER OF SCIENCE

in

ECOLOGY  
in the

OFFICE OF GRADUATE STUDIES

of the

UNIVERSITY OF CALIFORNIA

DAVIS

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2019

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*Abstract* - The conservation benefits imparted by marine protected areas (MPAs) are increased when reserve site selection is based on the spatial dynamics of exploited species. The spatial dynamics typically considered for siting often ignore ontogenetic movement patterns. The movement patterns of blue rockfish (*Sebastes mystinus*) have been categorized as limited. However, the basis for this categorization comes from studies taking place over timeframes that are too short to identify the possibility of ontogenetic movement. This limitation is addressed by using long-term fish surveys to construct a size distribution spread across depth. Individuals appear in high abundance in shallow water (<25m) and deep water (>35m). Individuals only begin to show up in deep water when they reach sizes associated with sexual maturity ( $\geq 19$ cm). These results show that *S. mystinus* shifts its habitat preference based on developmental stage. The ontogenetic movement exhibited by *S. mystinus* is drastic enough to influence the biomass benefits its populations receive from MPA implementation. The ontogenetic movement exhibited by *S. mystinus* could influence the expected biomass increases imparted by MPA implementation.

## Introduction

No-take marine protected areas (MPAs) have been increasingly implemented over the past several decades with the aim of increasing marine biodiversity and fisheries biomass (Wood et al. 2008; Worm et al. 2017). Currently, ~4% of the world's oceans are protected by MPAs and this growth is expected to continue (Worm 2017). Empirical and theoretical studies show that the biomass increases from MPAs are improved when reserve site selection is based on the spatial dynamics of exploited species (Francour et al. 2001, Apostolaki et al. 2002, Costello et al. 2010, Kellner et al 2014). These benefits increase when the MPA is sited over the spatial area that

fished size classes inhabit (Francour et al. 2001, Apostolaki et al 2002). Much of the spatial analysis of fish in MPAs has focuses on larval dispersal and spillover as drivers of spatial heterogeneity of populations (Grüss et al. 2011).

Another type of movement that may influence MPA efficacy is ontogenetic movement (Grüss et al. 2011). Many fish species exhibit ontogenetic shifts in their habitat use. This shift represents a key form of dispersal that results in spatial heterogeneity of a population (Gerber et al. 2005). Ontogenetic movement can be used to assess the efficacy of MPA siting decisions (Gerber et al. 2004, Gerber et al. 2005, & Grüss et al. 2011). One way to assess the efficacy of a proposed MPA siting for a spatially heterogeneous population is to conduct sensitivity analysis of a stage-structured population model (Gerber & Heppell 2004; Gerber et al. 2005; St. Mary et al. 2000). Ontogenetic movement integrates well with stage-structure models and spatial heterogeneity because it provides an understanding of the spatial distribution of each life-stage.

A challenge to incorporating ontogenetic movement into MPA design is the difficulty in elucidating this type of movement pattern. Fish movements are often tracked using electronic tags or capture-dependent surveys. Both methods present challenges for recognizing the presence of ontogenetic movement. The duration of electronic tag studies is often limited by the battery life of the tags. This makes it difficult to track movement of individuals over multiple life-stages (Thorstad et al. 2013). Capture-dependent surveys only provide a snapshot of an individual's location at a given time, meaning ontogenetic movement cannot be determined by tracking specific individuals (Thorstad et al. 2013). However, movements of a species can be implied through spatial heterogeneity of the abundance of various life-stages (Lucas & Baras 2000). This can only be achieved with a large amount of data. Due to these drawbacks, ontogenetic movement may go unrecognized in tracking studies.

Existing movement studies of blue rockfish (*Sebastes mystinus*) exemplify the challenges to identifying ontogenetic movement. Current work on *S. mystinus* demonstrates that individuals show little or no movement from their essential habitat: nearshore reefs (Gallagher & Heppell 2010; Lea, McAllister, & VenTresca 1999; Jørgensen et al. 2006; Reilly 2001). Individuals in nearshore reefs tagged with acoustic tags and passive tags provide evidence that the species maintains a small home range (Lea, McAllister, & Van Tresca 1999; Jørgensen et al. 2006; Miller & Geibel 1973). However, there were individuals that traveled many nautical miles in all of these studies. These individuals were treated as outliers for which no explanation was offered. A different acoustic tagging study attempted to explain these outliers by noting that *S. mystinus* exhibited periodic shifts in its home range (Green, Greenley, & Starr 2014). Beyond tagging studies, there is other evidence that *S. mystinus* shifts its home range. Commercial surveys show that the mean size of individuals changes with depth (Reilly et al. 1993). This is further supported by observations that juvenile *S. mystinus* rarely venture into deeper waters until 3 or 4 years of age; the onset of sexual maturity (Miller & Geibel 1973). Additionally, it has been hypothesized that the depth preference may be driven by differences in temperature preference; smaller fish preferring warm, shallow waters while bigger fish prefer cool, deep waters (Love, Westphal, & Collins 1985; Love, Carr, & Haldorson 1991). Taken as a whole, this suggests that there may be an unexamined ontogenetically-driven shift in depth preference between the juvenile and adult life-stages.

The ontogenetic movement of *S. mystinus* is important in the context of California's MPA network. The species makes up a large portion of the recreational marine catch in California (Dick et al. 2017; Miller & Geibel 1973). It is also one of the species that undergoes monitoring and assessment within the adaptive management framework of California's MPA

network (CDFW 2016; Kaplan et al. in press). Identifying ontogenetic movement in *S. mystinus* could bolster the precision of these assessments and provide a stronger understanding of the effect that California's MPAs have on the *S. mystinus* fishery.

To study the ontogenetic movement of *S. mystinus*, I utilized two multi-year surveys of nearshore habitat. By examining movement over a multi-year time frame, I hope to elucidate interannual movement patterns. Since younger individuals seem to have a depth limitation, I examine the patterns in size distribution across a range of depths. The specific objectives of this study are (1) determine whether or not there are differences in the size distribution of individuals across various depths and, if so, (2) determine the sizes at which individuals begin to shift to deeper waters.

## Materials & Methods

### **Data Collection**

This study is constructed using two surveys which sampled fish off the coast of California. The Partnership for Interdisciplinary Studies of Coastal Oceans (PISCO) conducted visual dive surveys of fish diversity in near-shore kelp forests from 1998 to 2016 (Hamilton et al. 2010; [www.piscoweb.org](http://www.piscoweb.org)). Divers followed 2mx2mx30m fixed-depth transects situated throughout the water column. These transects were located at depths ranging 1-30m. Within a transect, the divers counted and visually estimated the size of all fish encountered. There were 7,430 observations of *S. mystinus* in this dataset.

Beginning in 2007, the California Collaborative Fisheries Research Program (CCFRP) has conducted hook-and-line surveys of fish diversity both inside and outside of MPAs (Yochum, Starr, & Wendt 2011; [www.mlml.calstate.edu/ccfrp](http://www.mlml.calstate.edu/ccfrp)). Sampling is conducted with the

help of volunteer anglers who fish along drift transects. The transects vary from 5m to 54m deep, though *S. mystinus* was only caught as deep as 42m. All fish caught are measured using fish boards and then released. I used a subset of this dataset spanning 2007-2016 which has 38,681 observations of *S. mystinus*.

The two surveys overlap in the geographic region that was sampled. The overlap is situated in the central coast of California, with PISCO extending further north and south than CCFRP. PISCO surveys sampled from Santa Cruz to the Channel Islands. Sampling for CCFRP was conducted from Año Nuevo to Morro Bay.

The intra-annual timing of sampling differed slightly between the surveys. Sampling for CCFRP occurred during the summer months of July through September with a small amount of sampling continuing into October. There was year-round sampling by PISCO. However, most of the PISCO sampling effort was focused around the summer months of July through October. I used data collected July-September, the time when both surveys collected most of their data. By examining a single season, I controlled for seasonal environmental conditions that might influence intra-annual shifts in habitat preference.

### **Common index of abundance**

The first step was to approximate an index of *S. mystinus* abundance for each survey. This results in a common metric of abundance between the surveys and allows the datasets to later be combined.

#### *PISCO*

Counts per transect were used as the index of abundance for the PISCO data. The depth was consistent within a transect, so the individuals associated with a transect could easily be

assigned to that depth. The result was a size distribution for each depth sampled. Each size distribution at a particular depth was then divided by the number of transects sampled at that associated depth. This resulted in counts per transect for each size class and each depth.

### *CCFRP*

Catch per unit effort (CPUE) was used as the index of abundance for the CCFRP data. The depth at which CCFRP anglers were fishing varies within each transect. The start depth and end depth were recorded for each transect. All fish caught along a transect were assigned to that transect, not a specific location or depth along that transect. I made a few simplifying assumptions about this dataset: 1) each transect was fished along a flat depth gradient from the start depth to the end depth; 2) the vessel drifted at a fixed rate across the entire transect; 3) all fish have an equal chance of being caught at any depth along the transect.

Using the start and end depths for the CCFRP transects, the transects were broken into 1 meter depth segments. I assumed that the vessel drifted at the same pace across the whole transect, so all depths within a transect were sampled for an equal amount of time. I divided the time spent fishing a transect evenly across all depths sampled for that transect. This time was then multiplied by the number of anglers who were fishing for that transect. This process was repeated for all transects and then summed for each depth to get the total effort for each meter of depth sampled.

Using the assumption that a fish has an equal chance to be caught at any point along a transect, I assigned all catch from a transect to all depths sampled along that transect. This resulted in a size distribution for each depth sampled. These size distributions were divided by the total effort for the associated depth to calculate CPUE.

## **Combining Datasets**

PISCO and CCFRP used different sampling methods and sampled across a different range of depths. This means that they have a different magnitude of abundance and shape to their size distributions. To combine the size distributions into a single index of abundance, I needed to account for these differences.

First, I determine a size range where the shape of both distributions is similar. I looked at size classes for which both surveys observed a substantial number of individuals. Both datasets had a substantial number of observations for fish size 18-34cm. Within this range, I plotted the log-regression of various size intervals to find an interval for which both datasets had a similar slope. Slope was used because it indicated that the shape of the size distributions was similar even if the magnitude of abundance was not. The slope for the 19-27cm interval was similar for both size distributions.

Based on the 19-27cm size range, I calculated a conversion constant to bring both indices to the same magnitude of abundance. The conversion constant was determined by minimizing the difference between the two size distributions over the 19-27cm interval. After multiplying the datasets by the conversion constant, the size distributions were combined into a single distribution of sizes 2-49cm sampled over 1-42m depth (Fig 1a.).

## **Understanding the Overall Size Distribution**

To verify that the overall size distribution is representative of expectations from the natural population, the resulting size distribution was compared to a von Bertalanffy growth curve of *S. mystinus* (Fig 1a & 1b). The von Bertalanffy growth curve parameters used were  $t_0 =$

-1.145,  $t_a = 50$ ,  $L_{inf} = 38.15$ ,  $k = 0.172$  (Kaplan et al. in press). The peaks around 7cm and 13cm match the size of the year 1 and year 2 cohorts as expected by the von Bertalanffy growth curve.

### **Removing Size Effect**

Due to changes in mortality and growth rate with age, larger size classes are generally less abundant than smaller size classes. I removed the effect of survival across age to allow for comparisons of abundance across depth. To account for the noise in the data, I fit two regression lines for immature and mature individuals, respectively. The breakpoint was set at 19cm because this is the size at which individuals begin to sexually mature (Miller & Geibel 1973). These lines represent the mortality slope for the various size classes. The value of the regression line for the immature size classes was used as a baseline for mortality. To remove the size effect, I needed to bring the mortality slope of the mature individuals up to this baseline. This was achieved by creating a ratio of the baseline to the value of the regression line for each mature size class. The largest size classes had the lowest abundance, which means that the ratio to baseline abundance was orders of magnitude higher than the other ratios. The ratio for 37cm was applied to all size classes above 37cm to bring those ratios back down to the same order of magnitude. Each size class was then multiplied by its respective ratio to bring it up to the baseline value of abundance. The resulting values for abundance were then normalized to the baseline.

### **Results**

The two datasets can only be combined and treated as a single size distribution if they were sampled from the same size distribution. Before combining the PISCO and CCFRP

datasets, I examined the overlapping size region with a two-sided Kolomogrov-Smirnov test. The evidence fails to find that the data are sampled from different distributions ( $p < 0.05$ ).

The final combined size distribution controls for changes in mortality based on size. This allows for comparisons of abundance across depth. By examining the abundance of fish at each depth sampled, I show how the abundance of various size classes changes across depth (Fig. 2). Most noticeable in these size distributions is the presence of two major clusters of individuals. The greatest abundance of fish are present in shallow waters  $< 25\text{m}$  deep. A smaller cluster of individuals appears at depths  $> 35\text{m}$ . There is a distinct lack of individuals in the zone between  $25\text{m}$  and  $35\text{m}$ .

Examining the relative abundance of each size fish at each depth sampled allows for a higher resolution to elucidate the trends within the two cluster of individuals (Fig. 3). These trends are visualized using a heatmap showing relative abundance of each size class at each depth sampled. The valley of minimal abundance between the two clusters is much more obvious when the data is visualized in this way. The distribution of individuals in shallow water contains a high abundance of fish from all size classes. Individuals as small as  $11\text{cm}$  begin to move out of the shallow water clump. However, they are not present in sizable numbers until they reach  $19\text{cm}$ . At sizes  $\geq 19\text{cm}$ , the fish become more abundant in the deep cluster.

There is a distinct band of high abundance of fish in the  $34\text{-}37\text{cm}$  size classes. These size classes seem to be abundant throughout the entire depth range. Even though the abundance relative to other size classes is high, these size classes follow the same trend as other fish  $\geq 19\text{cm}$ . The  $34\text{-}37\text{cm}$  fish are most abundant in the shallow and deep clusters and are least abundant in the  $25\text{-}35\text{m}$  depth range.

A general additive model (GAM) relating abundance to size class and depth supports the findings that individuals are segregating into two distinct clusters. Both size and depth are significant predictors of abundance ( $p < 0.001$  &  $p < 0.01$ , respectively). The abundance response to depth peaks in the shallow cluster at 17m then begins to decrease (Fig. 4a). This decrease continues until 35m, where the response begins to increase again. This decline and subsequent increase correspond to the clusters of abundance observed on the heatmap.

## Discussion

The conservation benefits of MPAs can be increased when their siting takes into account exploited species movement patterns (Apostolaki et al. 2002, Palumbi 2004). However, ontogenetic movement is often overlooked because it can be difficult to identify (Grüss et al. 2011). I have examined the interannual movement patterns of *S. mystinus* to elucidate the presence of ontogenetic movement patterns. Analysis of the depth distribution of size classes revealed that individuals begin to move into deeper waters at the sizes associated with sexual maturity. This evidence supports the hypothesis that *S. mystinus* exhibits an ontogenetic movement pattern.

## **Habitat Preference**

The presence of two distinct clusters of individuals shows that individuals are seeking specific depth ranges rather than uniformly distributing across the depth range. There is an uptick in abundance of fish in the deep water cluster starting with the 19cm size class. *S. mystinus* males begin to sexually mature at 19cm while females begin to reach sexual maturity at 21cm (Lea,

McAllister, & VenTresca 1999). The sizes at which blue rockfish begin to appear in the deeper waters suggests that the shift in depth preference occurs at the onset of sexual maturity.

The band of high abundance for the size classes 34-37cm is likely an artifact of the method used to control for mortality. As the number of individuals present in the dataset declined, the ratio of abundance of the large size classes to the baseline size class increased dramatically. The 34-37cm size classes had conversion ratios that were orders of magnitude higher than the rest of the size classes. While I tried to control for this, these size classes still ended up having a high conversion ratio. This results in abundances that are much higher than the other size classes. Even though these size classes show a higher relative abundance, they follow the same trend of high abundance in the shallow and deep clusters with low abundance in between.

### **Drivers of Movement**

One possible explanation for the ontogenetic movement is changes in preference for habitat type. The shallow cluster of individuals is likely associated with nearshore kelp forests or reefs. It is well established that *S. mystinus* use this type of shallow, nearshore habitat as nursery grounds and it is essential habitat for the species (Gallagher & Heppell 2010; Miller & Geibel 1973; Jørgensen et al. 2006; Reilly 2001). Individuals tracked in deeper waters have been found to associate with rocky outcropping and rock pinnacles (Jørgensen et al. 2006; Miller & Geibel 1973). It is likely that the deep cluster of individuals is residing in these habitat types. It is unclear why individuals are not often found in the 25-35m depth zone. There may be a lack of suitable habitat in this area. However, those conclusions are outside the scope of this study. To

examine habitat type as the driver for the ontogenetic habitat shift, the next step would be to study the correlation between size classes and the habitat type where sampling occurred.

Another possible explanation for the ontogenetic movement is intraspecific competition that emerges at the onset of sexual maturity. *S. mystinus* switch their diet when they reach sexual maturity and larger fish maintain a larger territory (Love, Yoklavich, & Thorsteinson 2002; Lowe & Bray 2006). This may lead to increased intraspecific competition. Food availability driving interannual movement patterns is supported by current evidence that food availability drives intra-annual movement patterns. All size classes of *S. mystinus* exhibit a seasonality of movement associated with upwelling events and the availability of food those events bring (Hallacher & Roberts 1985). During upwelling events, when plankton abundance in nearshore waters increases, there is an increase in nearshore abundance of *S. mystinus* (Hallacher & Roberts 1985). This shows that food availability is a driver of intra-annual patterns of abundance. While this seasonality suggests a possible explanation for the observed clusters of abundance, it does not directly explain the ontogenetic movement. This is because all samples were taken during the summer to control for intra-annual variation.

### **Management Implications for California MPAs**

By failing to account for the ontogenetic movement of *S. mystinus*, estimates of MPAs' effects on *S. mystinus* biomass production are likely incorrect. *S. mystinus* play an important role in the California recreational marine fishery (Dick et al. 2017; Miller & Geibel 1973). The California fishery for *S. mystinus* is currently managed with a bag limit, but there is no lower size limit to the fish that can be kept (CFGC 2018). As a result, spatially explicit management practice, such as MPAs, are the only way to regulate *S. mystinus* catch based on life-stage. The

California coast has an MPA network comprised of 124 state marine reserves, state conservation areas, state marine parks, state marine recreational management areas, and special closures (CDFW 2016). Of these 124 zones set aside for protection, 104 stipulate no take of marine species within their borders (CDFW 2016). Many of these no-take MPAs span the entire depth range analyzed herein, offering protection for both deep and shallow habitats. However, there are seventeen MPAs that only protect shallow *S. mystinus* habitat and sixteen MPAs that only protect deep *S. mystinus* habitat (CDFW 2018). The shallow habitat MPAs' effect on *S. mystinus* biomass is likely overestimated because the estimates do not account for ontogenetic movement. While shallow habitats contain the full complement of *S. mystinus* life-stages, current understanding of the species' movement patterns assumes that the fish will remain in that area. However, I found that a portion of the adult *S. mystinus* are emigrating into deep waters. This would take them out of the shallow MPAs thereby reducing biomass in those MPAs. The MPAs that only protect deep habitat will experience the opposite effect. The effect that these MPAs have on *S. mystinus* biomass is likely underestimated because individuals were not expected to spend a considerable amount of time in deep water. The deep habitats contain only mature adults and those adults will mate. Since these MPAs do not contain suitable nursery habitat, the recruits produced in deep habitat MPAs will emigrate to shallow habitat. The deep habitat MPAs may be an important source of recruits for MPAs that protect shallow habitats. As California continues to assess the effectiveness of its MPA network, these assessments need to account ontogenetic movement in estimations of their effect on *S. mystinus* biomass.

## Conclusions

These findings serve as a framework for recognizing the presence of ontogenetic movement in fish species. Ontogenetic movement has been recognized in a number of fish species, yet it still remains an understudied movement pattern (Grüss et al. 2011). Here, I provide a method for elucidating ontogenetic movement using multi-year survey data. This method works well for recognizing movement patterns that occur over coarse horizontal spatial scales. Movement over fine spatial scales would be difficult to detect in aggregate. Additionally, some survey methods, such as hook-and-line, cannot detect vertical distribution. The biggest drawback of this method is that it requires a large amount of data collected over multiple years. The easiest way to overcome this hurdle is to leverage existing survey datasets. However, existing large-scale multi-year surveys, such as ecosystem monitoring datasets, may show a bias towards species that are economically, socially, or politically important (Powers & Monk 2010). This means that there is a bias in which species can be examined with this method unless additional data collection is undertaken.

Despite these drawbacks, large-scale multi-year surveys can make it possible to investigate ontogenetic movement in multiple species based off of a single community or ecosystem monitoring dataset. This can lead to the elucidation of ontogenetic movement exhibited by other fish species and subsequent integration of this information into MPA assessment. Theoretical models show that the importance of ontogenetic movement for a species in an MPA is not generalizable to other species (Gerber et al. 2005). This underlies the importance of studying and incorporating each species' ontogenetic movement independently. While this is a difficult proposition, failure to recognize these patterns may result in suboptimal implementation of MPAs (Palumbi 2004).

## **A Note on Deacon Rockfish**

For many years, *S. mystinus* was identified as having two distinct patterns of pigmentations known as ‘blue-blotched’ and ‘blue-sided’ (Frable et al. 2008; Hannah, Wagman, & Kautzi 2015). It was suspected that these two morphs represented subspecies of *S. mystinus* (Hannah, Wagman, & Kautzi 2015). In 2017, the National Oceanic and Atmospheric Administration declared these morphs to be unique species (Dick et al. 2017). The “blue-blotched” morph retained the name blue rockfish while the ‘blue-sided’ morph was classified as a new species called deacon rockfish (*Sebastes diaconus*). This reclassification of *S. mystinus* as two separate species calls into question the validity of conclusions drawn from data which conflated the species. The reclassification was anticipated by CCFRP, which began distinguishing between the two *S. mystinus* morphs in 2011. Using 2011-2016 CCFRP records, I constructed size distributions and depth distributions for each species. I found that the shape of the size distributions was similar. The depth distributions showed similar trends, as well. Furthermore, the number of *S. diaconus* observations was a small fraction of the *S. mystinus* entries for that time period. This leads me to believe that using conflated data collected prior to the reclassification does not affect the conclusions drawn about *S. mystinus* herein.

## Acknowledgements

I would like to thank Louis Botsford, Marissa Baskett, and Jim Sanchirico for their excellent guidance. California Department of Fish & Wildlife and University of California, Davis for funding. Lauren Yamane and Katherine Kaplan for modelling guidance. Duncan Lang for coding and statistical advice. The Partnership for Interdisciplinary Studies of Coastal Oceans (PISCO)

and the California Collaborative Fisheries Research Project (CCFRP) for access to their data which was the basis of this study.

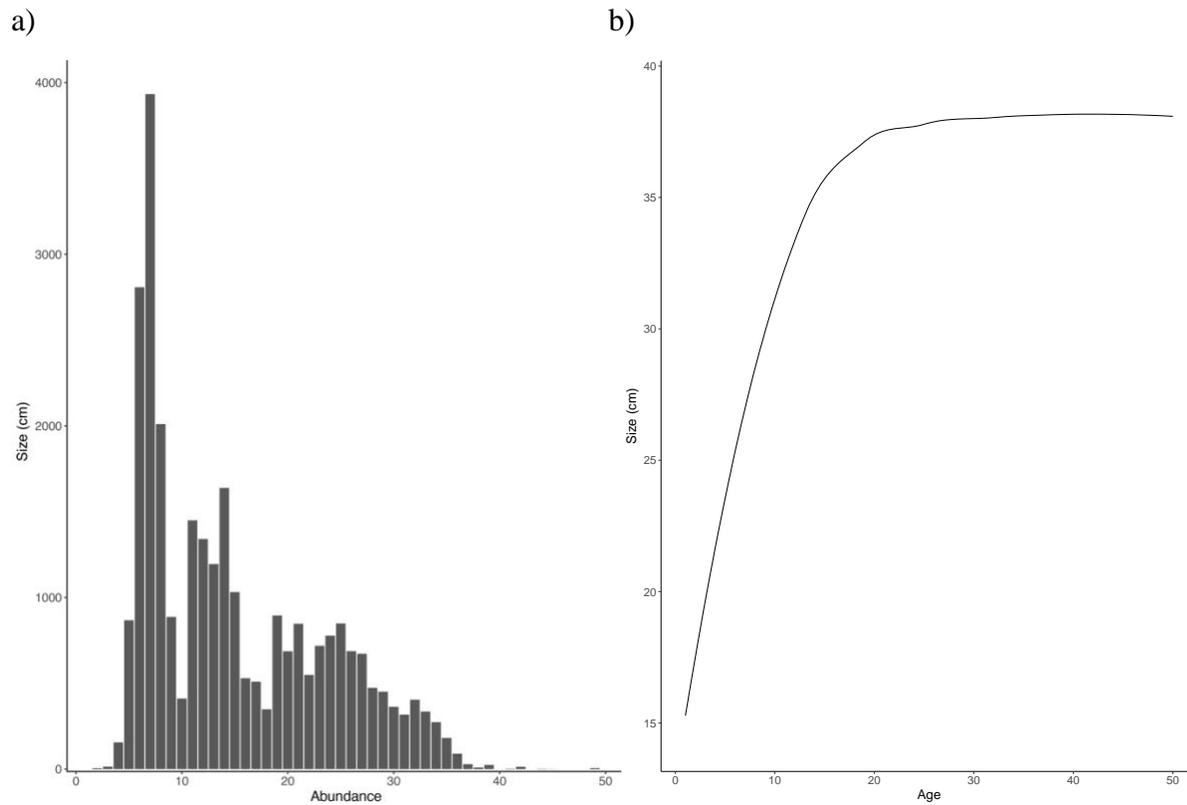
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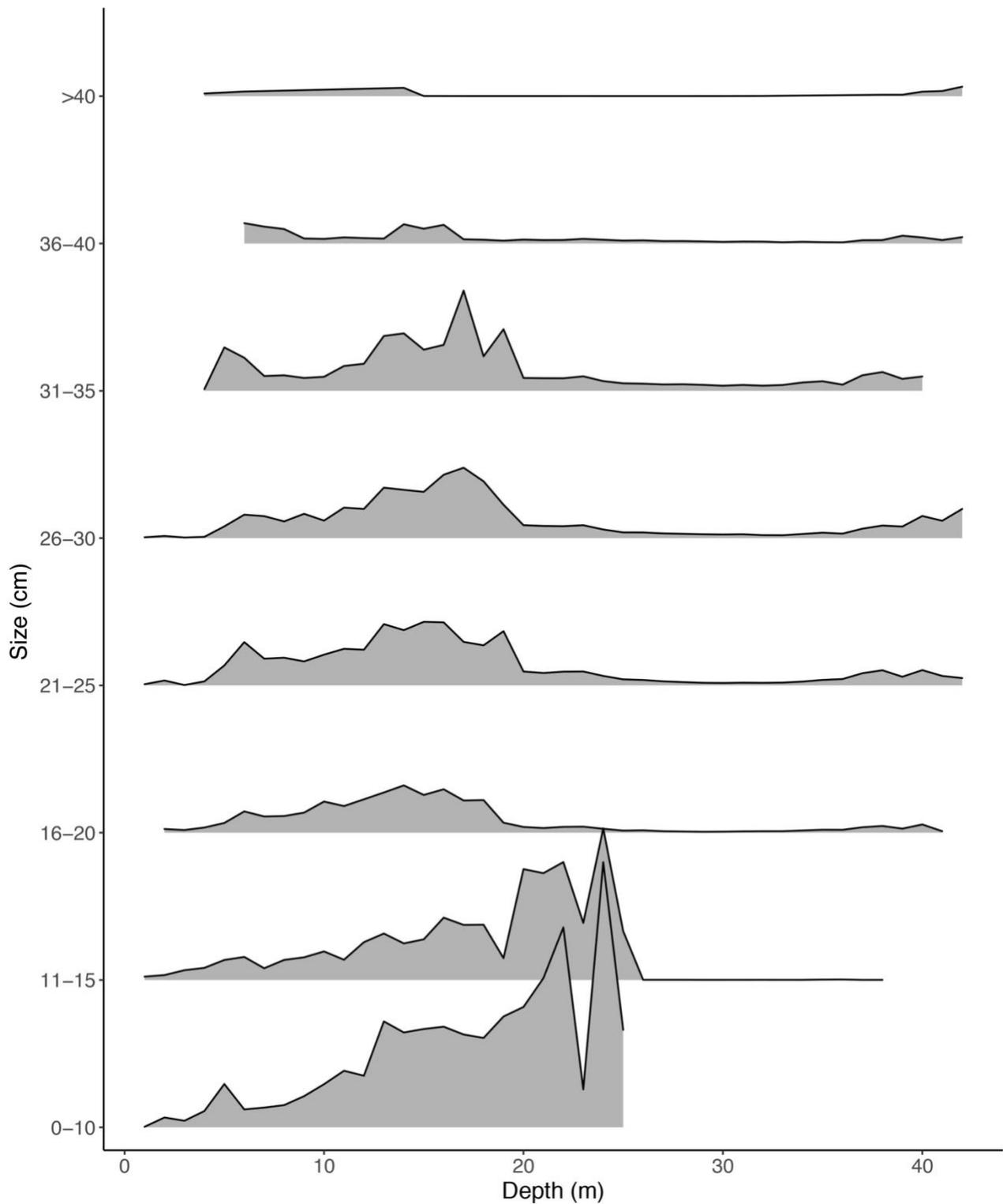
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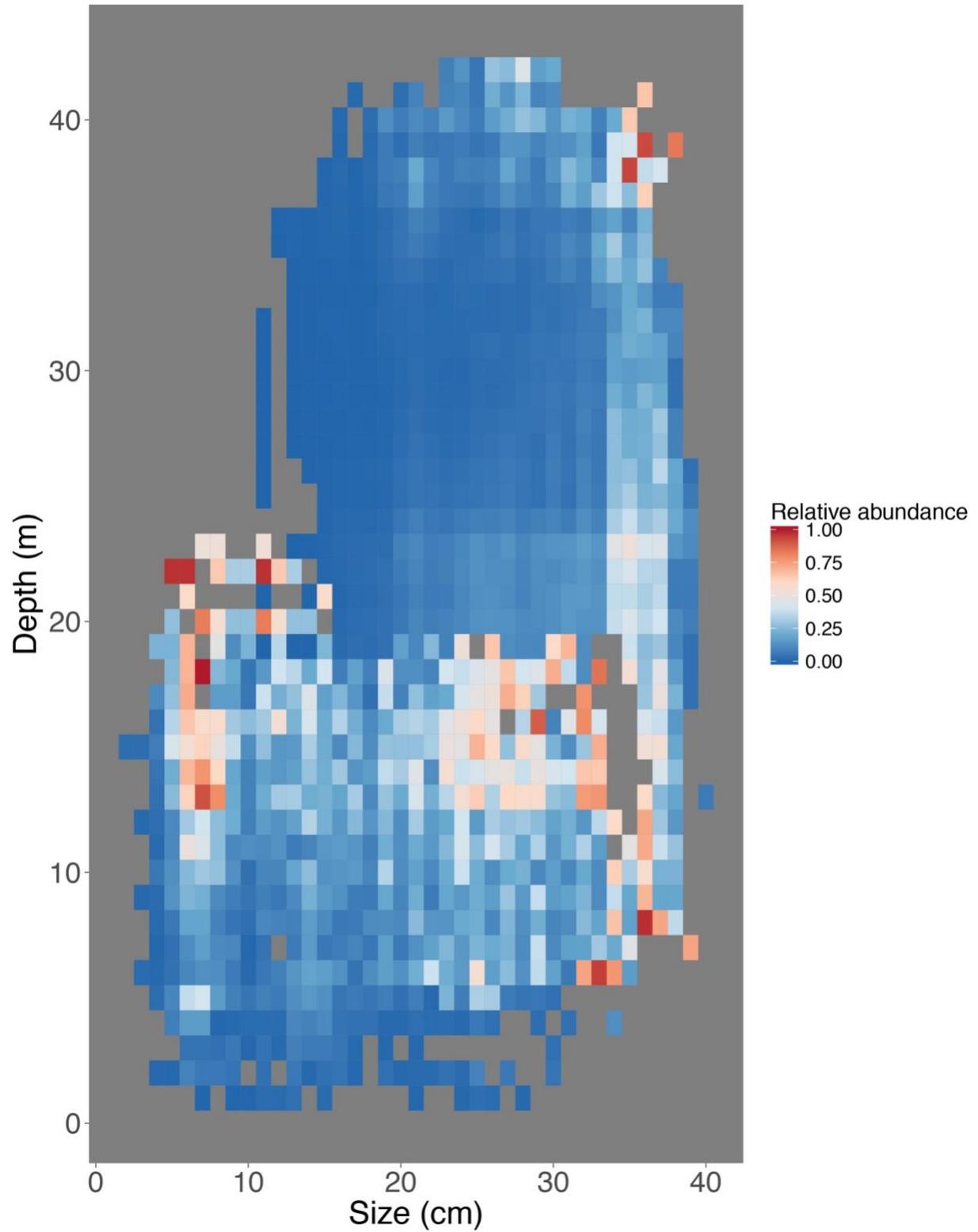
## Figures



**Figure 1.** a) Size distribution constructed by combining hook-and-line survey data with visual dive survey data. b) Von Bertalanffy growth curve with 1 SE shaded region. Year 1 and year 2 cohort peaks on the size distribution correspond with the sizes at age 1 and 2 on the von Bertalanffy growth curve. This verifies the combined size distribution conforms with expectations of the natural population size distribution.

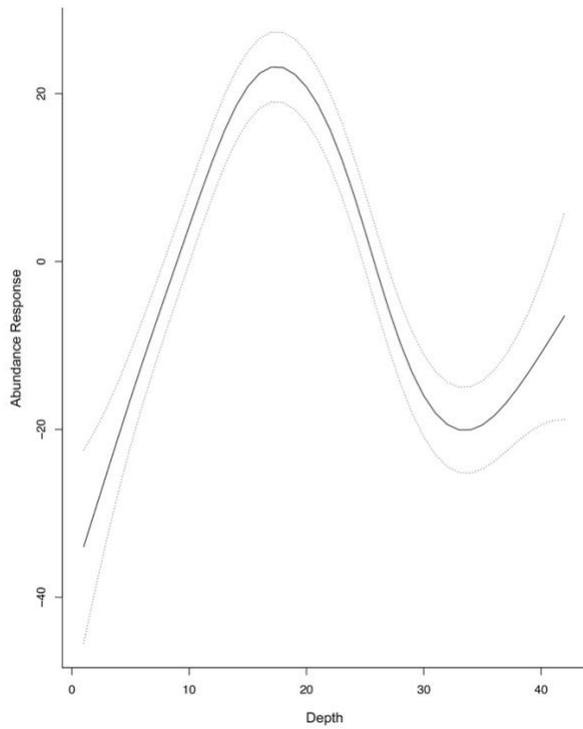


**Figure 2.** Abundance of various size classes distributed across depth. Size of the peaks shows relative abundance of individuals. There are two distinct clusters of individuals at depths <25m and >35m.

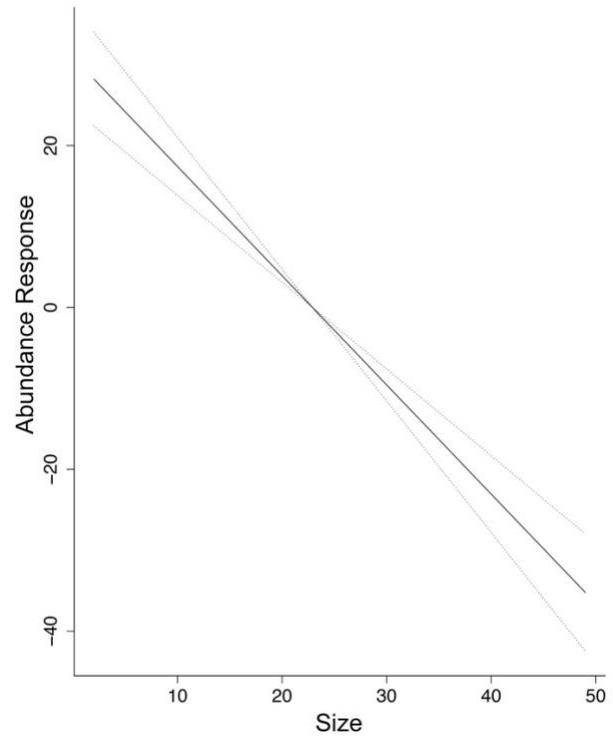


**Figure 3.** Heatmap showing the relative abundance of each size class of fish at each depth sampled. The data was log-transformed and cutoff at values below mean + 2SD for better resolution.

a)



b)



**Figure 4.** GAM partial response curves of abundance to a) depth and b) size. The shape of the depth response highlights the decline in abundance that occurs at 25-35m and the subsequent increase in abundance at 35m. Abundance shows a steady decline with size. Dashed lines shows 1 SE.