



Inter-annual variability in forage fish population size structure: Comparison of selectivity of traditional vs. non-traditional sampling devices

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ABSTRACT

Despite the crucial role of forage fish in ecosystem functions globally, data on population demographic structure are often not readily available for many forage fish stocks. Data to characterize variability in population size structure can be highly informative for population monitoring and management, as such data can be used to estimate cohort strength and recruitment, variation in growth rates, and for body-size dependent broadcast spawners such as anchovy, variation in reproductive capacity. In this study, Anchovy Length Indices (ALI) were developed for the central California portion of the central stock of Northern anchovy using predator- and trawl-derived samples. Five different data sources were examined: seabird, sea lion and salmon diet, and midwater and acoustic-trawl surveys. Seabird and midwater trawl surveys had the longest time-series of data. Seabird and midwater trawl methods differed somewhat in their relative selectivity patterns, yet both sampled all age classes of anchovy and reflected similar patterns of inter-annual variability in length frequency. The combined seabird-trawl ALI (1998–2017) was used to characterize anchovy size structure for years when the fishery was not sampled (< 2014). The overall bimodal distribution of anchovy size was divided at 94 mm, suggesting that separation of age 0 and age 1+ anchovy in central California in summer (June) during this timespan was smaller than historic means for the region. The predator-based ALI provided further information prior to the initiation of anchovy length sampling during midwater trawl surveys (1993–1997). The ALIs encompassed periods of extremely high and low anchovy biomass, as well as extreme warm and cold ocean climate events; small mean anchovy lengths appeared to be related to warm conditions (ENSO).

1. Introduction

Inter-annual variability in the size structure of forage fish populations is a reflection of cohort strength (year-class size) and variable growth rates. These factors are affected by both top-down and bottom-up processes. Predation mortality in the marine environment is generally size-specific (Peterson and Wroblewski, 1984; Sogard, 1997). Growth can be influenced by oceanographic factors such as the El Niño Southern Oscillation (ENSO; Butler, 1989; Fiedler et al., 1986), although changes are likely directly driven by prey availability (Butler, 1989). Growth rates of late-stage forage fish larvae and early juveniles may affect the magnitude of recruitment (Smith, 1985) and adult size (Parrish et al., 1986). For example, off of southern Baja California, Mexico,

the asymptotic size of northern anchovy (*Engraulis mordax*) was shown to be almost entirely determined by juvenile growth, with minimal growth after 18 months (Parrish et al., 1985). Following the temperature-size rule (Atkinson, 1994), historical studies show that anchovy off southern California are middling in size and central California anchovy are larger (Mais, 1974; Mallicoate and Parrish, 1981; Parrish et al., 1985). More recent data from the Columbia River Plume region (Oregon, Washington) suggest even larger anchovy further north (Litz et al., 2008). Batch fecundity is a function of body size in broadcast spawners such as anchovy; therefore, population size structure influences reproductive capacity (Parrish et al., 1986).

Accurate demographics are often not well quantified for many forage fish populations, unless they are the subject of directed fisheries or

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surveys (Piatt et al., 2018). Even then, fisheries biases exist due to effort and gear types. Sampling challenges include the cost and effort of establishing a proper spatio-temporal sampling scheme for species with typically patchy distributions. Although the concept of non-traditional, predator-based sampling is not new (e.g., Cairns, 1992), implementation of this approach is not widespread. If prey species and size selectivity can be quantified, predators can potentially provide valuable data for fisheries assessment models and management (Einoder, 2009; Zador and Yasumiishi, 2016). Predator-based sampling has thus been used to study variation in fish abundance (Mills et al., 2007; Sydeman et al., 2017), community structure (Piatt et al., 2018), energy content (Wanless et al., 2005, 2018), body condition (Davoren and Montevecchi, 2003; Thompson et al., 2019), and size (length; Wanless et al., 2004). Examples of stock assessments utilizing predator information are the U.S. West Coast shortbelly rockfish (*Sebastes jordani*) stock assessment which directly incorporated juvenile rockfish abundance and length data from seabird and sea lion diets (Field et al., 2007a; Field et al., 2007b), and assessments of krill abundance in Antarctic waters which used size composition data inferred from penguin food habit studies (Reid and Brierley, 2001).

Data that inform fisheries assessment models with respect to changes in size and age structure are critical to evaluating variable recruitment in populations as well as estimating the effects of fisheries removals on demographic structure and abundance. To apply such compositional data, most fisheries stock assessments use an underlying population model together with length or age composition data from fisheries or surveys to estimate a selectivity function that quantifies the relative probability that fish of a given size (or age) are captured by a fishery gear type or predator (Sampson, 2014). This allows for comparisons of length composition data among surveys, fisheries, or other data sources to the models' prediction of population length compositions, adjusting for differences in size-based vulnerability of each sampling technique. Size-frequency distributions also often are converted to age-frequency distributions, based on previously determined relationships between age and length, allowing for use of age-structured models. Although the current study does not estimate an actual selectivity curve for northern anchovy, as this would require an associated population model, the intent is to evaluate the suitability of predator-derived length composition data relative to fisheries survey data to best inform the utility of these data sources (Reid et al. 1996; Reid et al. 2001).

Northern anchovy are the single most important forage species in the central-southern California Current Ecosystem (Szoboszlai et al., 2015; Koehn et al., 2016), in part due to their small size, presence in the epipelagic realm, nearshore distribution, and high energetic content. The central subpopulation is the primary stock of northern anchovy (CSNA) in U.S. waters. It ranges from central Baja California to north of Point Reyes, California (Smith and Lasker, 1978; MacCall et al., 2016), with core populations centered in the Southern California Bight and in central California around Monterey Bay (Parrish et al., 1986; MacCall, 1990; Bakun, 2014; Davison et al., 2017). Stock assessments were conducted regularly for the central subpopulation of northern anchovy (CSNA) until the mid 1990s when the population dipped below an established fisheries management threshold of 300 K mt (Jacobson et al., 1995) and resulted in closure of the primary directed fishery. Since then, anchovy has supported a low-yield fishery¹. The California Department of Fish and Wildlife (CDFW) curtailed the collection of length and age data in the mid 1980s, but subsequently resumed size/age analysis of fishery landings in 2014. Consequently there is a multi-decade gap in length/age composition data.

The lack of size/age data complicates the interpretation of various sources of abundance data, limiting our understanding of population dynamics. For example, abundance estimates from egg and larval

indices indicate that the CSNA stock increased dramatically to a 2005–2006 peak of over 2 million metric tons, before declining just as rapidly to a relative abundance level of less than 100,000 mt within several years (MacCall et al., 2016; Thayer et al., 2017). These dynamics are consistent with the long-held interpretation that variable ocean conditions are key drivers of population fluctuations for northern anchovy, as well as other coastal pelagic species in the California Current (Soutar and Isaacs 1974, Baumgartner et al. 1992, Checkley et al., 2017).

Northern anchovy exhibit differential life history characteristics (e.g., growth rates, sizes at maturity) north and south of Point Conception (Mais, 1974; Mallicoate and Parrish, 1981; Parrish et al., 1985, 1986). In this study, we assembled traditional and non-traditional data for the CSNA length frequency in the central California region, by comparing and combining predator-based samples and research trawl samples. We tested the hypotheses that 1) the selectivity patterns of predators and trawls differs, as trawl data come from distinct stations whereas predators target forage patches, but that 2) inter-annual variability in size structure of anchovy reflected by predators and trawls is similar. We then developed a robust estimate of length for the population and a time-series of size composition to characterize length-frequency changes during periods of highly variable biomass estimates.

2. Methods

2.1. Data sets

To reconstruct anchovy length distributions, we used three primary data-sets: rhinoceros auklet (*Cerorhinca monocerata*) diet datasets from Año Nuevo Island (ANI) and Southeast Farallon Islands (SFI) spanning the years 1993–2017, and anchovy length measurements from the National Marine Fisheries Service (NMFS) Southwest Fisheries Science Center's annual Rockfish Recruitment Ecosystem Assessment Surveys (RREAS) between 1998–2017 (Sakuma et al., 2016). SFI (37° 42' N, 123° 00' W) is located on the outer continental shelf, 29 km south of Point Reyes, California, whereas ANI (37° 06' N, 122° 20' W) is located ~ 1 km offshore, 35 km north of Monterey Bay (Fig. 1). The RREAS core sampling stations span the birds' foraging range (see Kato et al., 2003; McFarlane Tranquilla et al., 2004) from both sites, from Point Lobos south of the Monterey Peninsula, to north of Point Reyes, at bottom depths of ~ 50 to > 200 m (Fig. 1). Approximately 30 anchovies were sub-sampled for length from each positive haul during RREAS midwater trawl surveys conducted in May–June. Anchovy was sampled from adult birds at breeding colonies when they returned carrying prey to feed their chicks primarily in June–July. Specifically, rhinoceros auklets bring fresh intact prey to their chicks nightly that can easily be sampled (see Thayer and Sydeman, 2007 for details). Rhinoceros auklets can forage to 60 m although most dives are shallower (Burger et al., 1993; Kuroki et al., 2003), and midwater trawls sample at approximately 30 m depth.

To control for sampling date, we adjusted all individual fish length measurements to a standardized date of June 26 (mean sampling date for seabird and trawl data sets, treating unique sampling days as a unit; total range in Julian days: 118–219; trawl range: 118–169; ANI range: 161–219; SFI range: 166–211). No ageing was conducted. From visual assessment of growth data in the literature, we assumed linear growth of individual anchovy was reasonable at specified rates based on biological stage and adjusted individual length measurements accordingly (larval growth during the first ~75 days to a standard length (SL) of 35 mm, juvenile growth during days ~75–365 at 35–100 mm SL, and adults >100 mm SL at 20 mm per subsequent year (Mais, 1974; Hunter, 1976; Methot, 1981; Butler, 1989; Parrish et al., 1985, 1986; Mallicoate and Parrish, 1981).

The relative abundance of individually-measured anchovy standard length values in each trawl haul or from each bird sampling date was expanded by the total catch for that haul/date. Due to some low sample size years, we used years with $n \geq 8$ measured fish per source for

¹ <https://www.wildlife.ca.gov/Conservation/Marine/Pelagic/Northern-Anchovy-Landing>.

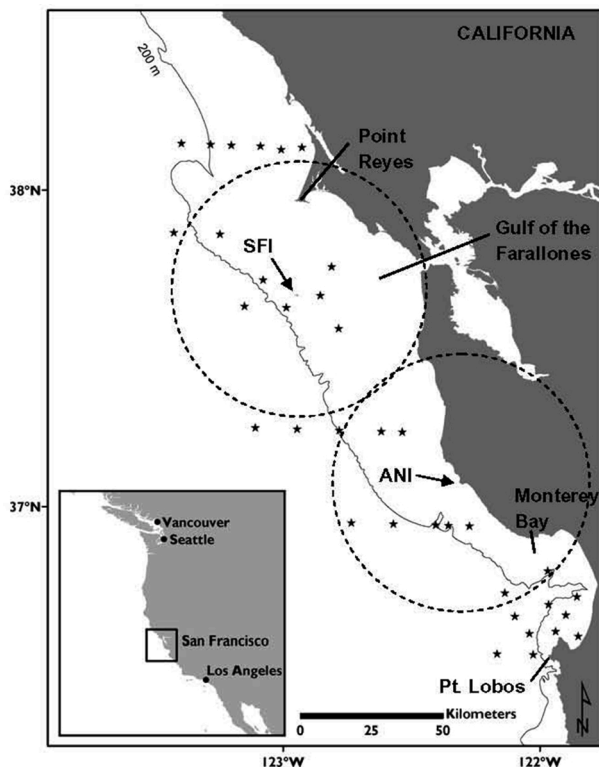


Fig. 1. Map of study area in central California with National Marine Fisheries Services trawl sampling locations (stars) and the estimated average foraging ranges of rhinoceros auklets from Año Nuevo Island (ANI) and Southeast Farallon Island (SFI; Adapted from Thayer and Sydeman, 2007).

inclusion in figures, and $n \geq 28$ for inclusion in statistical analyses (the natural breaks revealed upon data examination; for ANI & RREAS; Table A1). SFI data, however, regardless of sample size, were always combined with ANI data, not only to better reflect the spatial extent covered by trawl sampling (Fig. 1) but specifically to reduce a potential bias toward offshore fish introduced by SFI samples alone. This decision followed the logic that rhinoceros auklets breeding at ANI forage from their inshore starting point until encountering prey offshore, while auklets starting at offshore SFI sometimes forage only offshore when prey are available there, and not inshore (also see tracking data in Wilkinson et al., 2018). Therefore, ANI auklets are more consistently sampling a geographic region that represents the more nearshore distribution of anchovy (Mais, 1974; MacCall, 1990; Santora et al., 2014), and the distribution indicated by RREAS survey results (Fig. A1).

Sufficient data for statistical analyses existed in 1998–2000, 2004–2007 and 2015–2017 (Table A1). Bird data only were available for 1993–1997, 2001–2002, and 2008. Trawl data only were available in 2003. The years 2010, 2011 and 2012 were dropped completely due to extremely low sample size. For remaining low sample size years, we examined the spatial distribution of samples. Years with seabird data from ANI only (see Fig. 1) were 2001 and 2017; although SFI samples existed in 1997, 1998, 2009 and 2013, sample sizes were low. For RREAS trawl data, in two years with $8 > n < 28$ samples were spatially clumped. In 2009, there were three trawl stations containing anchovy all of which were located in the Gulf of the Farallones (June 14–15; in contrast to birds that year primarily sampling anchovy further south near ANI, albeit later in the season, June 25 and July 13, 20). In 2014, three trawl stations containing anchovy were all located in Monterey Bay (Fig. 1). These two years of trawl data, however, were utilized only for graphical depiction and not included in statistical analyses. Distribution of trawl stations containing anchovy was wider in years with $n \geq 28$.

We further supplemented the primary time-series with shorter datasets obtained from a fish predator, a mammal predator, and acoustic trawl surveys (Fig. A1). Chinook salmon (*Oncorhynchus tshawytscha*) diet was sampled from the Gulf of the Farallones during April–September 2005–2007 (Thayer et al., 2014). California sea lion (*Zalophus californianus*) diet at ANI was collected during April–August in 2010 and 2013–2016 (Robinson et al., 2018). The NMFS Coastal Pelagic Species acoustic trawl sampling was conducted in spring and/or summer of 2006, 2008, and 2012–2015; we used data between 36.8–39.5 °N². These supplemental data were used to ground-truth our longer time-series, especially during low sample-size years; these values were also standardized to June 26 and were used only for visual interpretation and not in any analyses.

An important assumption in this study is that these predators generally sample prey in proportion to what is available in the environment. Comparisons of prey abundance in predator diet with fisheries-independent trawl catch-per-unit-effort show similarities, for example, for rhinoceros auklets (Thayer and Sydeman, 2007), sea lions (Robinson et al., 2018), and Chinook salmon (Thayer et al., 2014).

2.2. Statistical analyses

Using individually-adjusted values, we tested for differences between anchovy length composition from seabird diet data (combined ANI and SFI) and trawl data. For all years combined, we characterized anchovy sizes at the population peaks of presumed juveniles (< 100 mm; Parrish et al., 1985) versus adults from kernel density estimates. Inter-annual data was compared using an analysis of variance (ANOVA) with an interaction term for year ($n \geq 28$ per sample type). ANOVA was weighted by effort as defined by number of sampling days for each source. Linear regression weighted by sampling days was used to compare mean anchovy length from trawl and seabird (mean of ANI and SFI means) datasets, and tested for autocorrelation using a Durbin-Watson test (Savin and White, 1977). A post-hoc Tukey test was used to compare annual means. Kolmogorov-Smirnov tests allowed further investigation of annual differences in anchovy length distributions between sampling types (Starr et al., 2016). However, the Kolmogorov-Smirnov test may not be robust to distributions that are not continuous, such as ours containing repeated measures. Therefore we defined the distribution function based on step values created by the empirical cumulative distribution, to avoid “ties” in the data and then ran the test on this function. All analyses were done in R v. 3.3.3 (R Core Team, 2017). To capture inter-annual variability in anchovy length, we create yearly Anchovy Length Indices (ALI) using mean anchovy lengths. Due to the varying time-series lengths, we propose two separate indices; the longest possible using seabird diet data (Seabird ALI: mean of pooled ANI and SFI data; 1993–2017), and a shorter time-series that used both seabird and trawl data (Seabird + Trawl ALI: mean of seabird index and trawl means; 1998–2017).

3. Results

Trawls and seabirds sampled similar lengths of northern anchovy overall. Central California anchovy sampled by trawls ($n = 4,327$) ranged from 18–160 mm (mean 108 mm, standard deviation 32 mm; Fig. 2). Seabirds sampled 32–162 mm anchovy ($n = 2,284$, mean 100 mm, standard deviation 30 mm). Adjusting for sampling date, extrapolating measured fish sampled by each method to the total catch, and using the ten years for which there were sufficient sample sizes for statistical comparison, the mean remained consistent for trawl samples but the range changed slightly ($n = 33,231$, range 30–161 mm SL).

² NOAA-Fisheries/Southwest Fisheries Science Center, CPS Trawl Life History Specimen Data, ERDDAP Version 1.82, <https://coastwatch.pfeg.noaa.gov/erddap/index.html>.

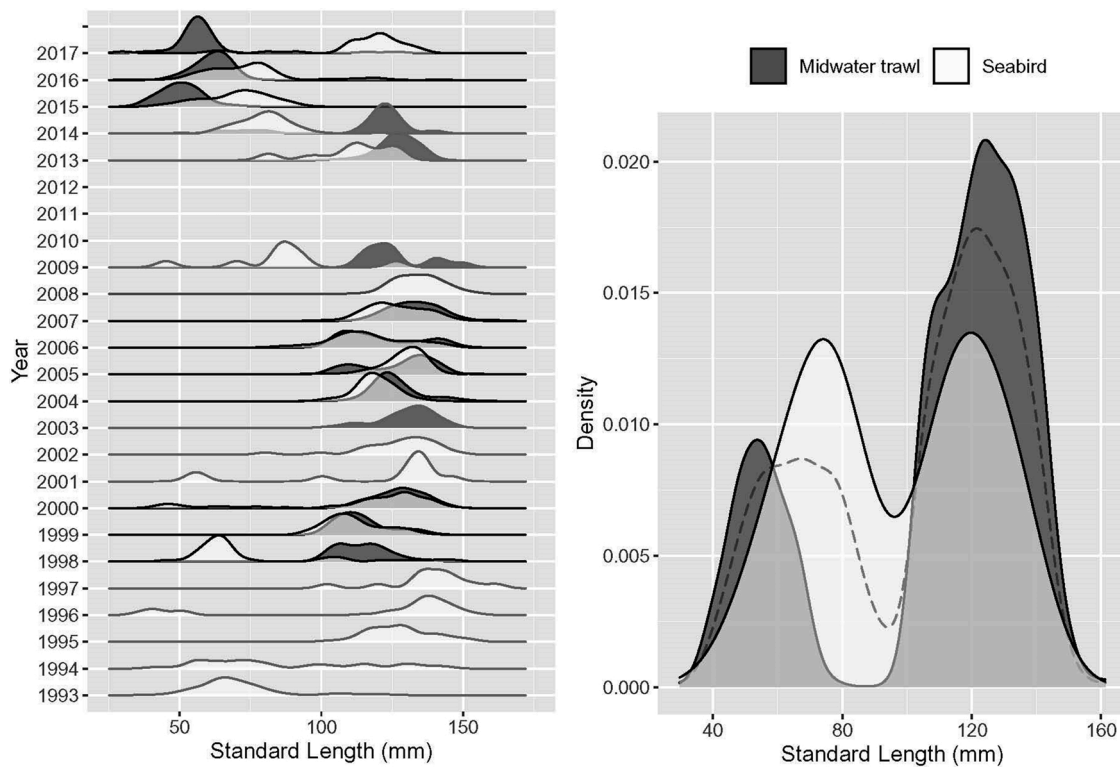


Fig. 2. Smoothed density distributions of yearly anchovy length measurements standardized to a common date A) annually from seabird and trawl data and B) overall for years with data from both sources, 1998–2017. The weighted and combined distribution is depicted with a dashed line. Years used in statistical analysis are outlined in black. Note: seabird diet data from 1997, 1998, 2001, 2009, 2013 and 2017 are from ANI only.

Values decreased somewhat for seabirds ($n = 1,567$, mean = 97 mm, range 30–155 mm SL). Overall, there was a significant difference in mean length between sampling type ($F_1 = 5.61$, $p = 0.02$); however, a highly significant interaction with year revealed that these differences between sampling methods were year-dependent ($F_9 = 277.76$, $p < 0.001$).

While annual anchovy length frequencies often consisted of only one peak (Fig. 2A), length frequencies from all years combined were bimodal for each sampling type (1998–2017; Fig. 2B). In other words, characterization of presumed juvenile versus adult sizes was not possible on an annual basis, but this characterization was useful for the population overall. The juvenile peak of the weighted and combined distribution for both seabirds and trawls was 67 mm, consisting of a juvenile peak of 74 mm as sampled by birds and 54 mm from trawls. Note that seabirds sampled visible proportions of juveniles in 10 years of the timeseries, while trawls sampled substantial juveniles in only 3 years (2015–2017; Fig. 2A). The adult peak overall was 121 mm, which was very similar between sampling types (mean_{bird} = 120 mm; mean_{trawl} = 124 mm). The trough minimum between peaks for combined data was 94 mm (Fig. 2B), 96 mm for bird samples and 87 mm for trawl samples.

Further investigation of annual differences was undertaken using Tukey tests on means and Kolmogorov-Smirnov tests on frequency distributions. Length distributions were not significantly different in 2000 ($p > 0.05$), and marginally significant in 1999; by contrast distributions were most different in 1998, 2015, and 2016 (Table A2). In some years statistical differences were due to slight disparities in length frequencies between source data (e.g., 2004–2007; Fig. 2). Mean anchovy length did not differ between sampling methods in 1999 and 2005 (< 3 mm; Table A2). There were small yet significant mean differences (< 7 mm) in 2004, 2006 and 2007. There was a larger mean difference (15 mm) in 2000 due to some juvenile fish sampled by seabirds, while in 2015 and 2016, seabirds sampled larger fish than trawls (13–20 mm mean difference). Relative selectivity differed most in 1998 when seabirds

sampled much smaller fish than trawls, and in 2017 when seabirds sampled substantially larger fish than trawls (38 mm and 52 mm mean differences, respectively).

Inter-annual analysis revealed a significant linear relationship between mean anchovy lengths sampled by seabirds and trawls ($N = 10$ years, $n_{\text{year}} \geq 28$, $R^2 = 0.65$, $p = 0.005$; Fig. 3). While some autocorrelation in the time-series was expected as anchovy cohorts moved through time, a Durbin-Watson test indicated minimal effect ($DW = 1.40$, $p = 0.09$).

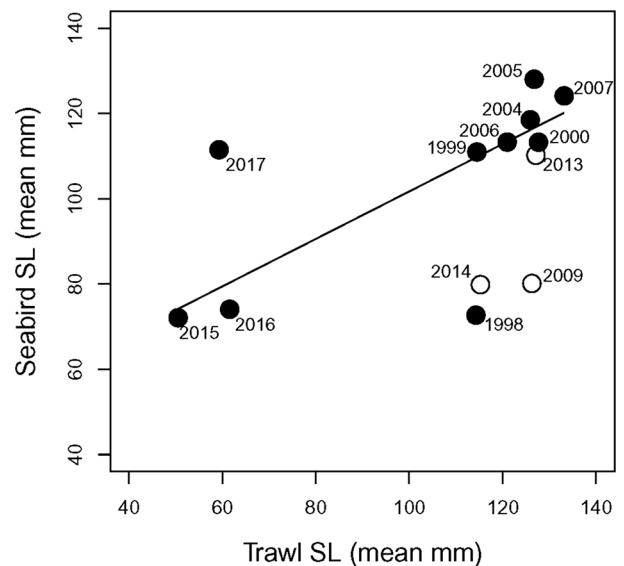


Fig. 3. Comparison of yearly mean anchovy standard length (SL) measurements from seabird diet samples and trawls. Filled points represent values from years used in statistical analyses ($n_{\text{year}} \geq 28$).

The two Anchovy Length Index (ALIs), one using only seabird data and the second using combined seabird and trawl data, revealed a similar pattern of covariance, punctuated by some relative selectivity differences between sampling methods (Fig. 4). Seabird-only values were generally the same or slightly lower than the combined seabird-trawl index values prior to the anchovy population crash in 2009, but differed considerably during the 1998 ENSO. There were greater differences during years of low anchovy biomass (2009–2014, Thayer et al., 2017; albeit low sample sizes of length frequencies in these years). Subsequently, the seabird-only index exhibited somewhat larger values than the combined seabird-trawl index in years during population recovery 2015–2017, (Fig. 4; Table A2; Zwolinski et al., 2019; Thayer et al., 2017; Sydeman et al., 2020).

The additional anchovy length datasets (i.e. predatory fish diet, mammal diet, and acoustic-trawl samples) varied in their concordance with the seabird diet and midwater trawl data. Mean anchovy lengths from fish diet samples (2005–2007) were closely aligned with seabird and midwater trawl values (Fig. 4). Mean anchovy lengths in acoustic-trawl samples were within 5 mm of seabird or midwater trawl samples in three years but > 13 mm in the remaining year with data. Mammal diet samples showed relatively poor agreement by comparison, falling between means of seabird and midwater trawl values in only one year (mean difference of 6 mm from seabird samples), and mean > 19 mm difference from seabird or midwater trawl samples in the three other years of data. Mammal diet samples, however, provided the only data in 2010 with sufficient sample size, and reflected small mean anchovy lengths (< 100 mm).

Overall, CSNA length frequencies in central California exhibited high variation in 1994–1998 and 2009–2017. Small mean anchovy sizes were observed in 1993–1994, 1998, 2009–2010, and 2014–2016. Many larval-sized fish (< 35 mm; Butler et al. 1989) were observed in 2015, and larval fish were also sampled in 1993, 1996, and 2016–2017.

4. Discussion

4.1. Indicators

Seabird and midwater trawl sampling methods appeared to differ somewhat in their relative selectivity, yet both methods appeared to sample comparable size classes of anchovy. Furthermore, seabird and

trawl methods revealed similar inter-annual variability in size of anchovy, suggesting that both sources may be valuable for informing estimates of recruitment and cohort strength. This consistency allows for the non-traditional data source, seabird diet sampling, to be used in development of indicators of inter-annual variability in anchovy population size structure. Non-traditional sampling is especially important in situations where data are not available from traditional fishery-dependent or -independent sources (Piatt et al., 2018; Thompson et al., 2019). Indicators of size and body condition (mass/length) have been developed for other forage species, capelin (*Mallotus catervarius*) and Pacific sand lance (*Ammodytes personatus*), sampled by rhinoceros auklets in the Gulf of Alaska where no traditional data sources exist (Thompson et al., 2019). Sunada et al. (1981) recorded high overlap in anchovy size data between brown pelican (*Pelecanus occidentalis californicus*) diet and fisheries landings in 1980 in southern California and suggested pelican diet sampling as a promising indicator of age and length structure of CSNA. Unfortunately, pelican diet sampling was not continued consistently. Rhinoceros auklet diet has been consistently collected in central California. Thus our seabird index of anchovy size starting in 1993 and our seabird-trawl index starting in 1998 span a time period when anchovy were not otherwise sampled in the California Current.

While we did not directly estimate age (e.g., count otolith rings), the overall bimodal distribution of anchovy size was divided at 94 mm for our sampling suggesting this as the separation between age 0 and age 1+ anchovy in central California in summer (June; Fig. 2B). Interestingly, this size distinction corresponds better to historical landings and trawl survey data from southern California (roughly 100 mm; Parrish et al., 1986; Mais, 1974), compared to historic fisheries-independent trawl surveys in central California showing a general 0–1 age-class separation at roughly 110 mm (i.e., larger fish at age; Mais, 1974). Mallicoate and Parrish (1981) suggested separation between ages 0 and 1+ of roughly 115 mm from central California landings data during August from 1966–1977. However, central California landings of age-0 fish in 1954 had a mean length of roughly 95–100 mm in August (Miller et al., 1995). Anchovy biomass in 1954 was extremely low (< 100 K mt) compared to the other study periods mentioned above (spanning various intervals between 1966–1984) when anchovy biomass ranged from 318 K mt (long-term median biomass) to > 2 M mt (Thayer et al., 2017; Sydeman et al., 2020; Table A3). Biomass was again extremely low during 8 years of our 25-year study (< 100 K mt, 1998 and 2009–2015) and < 318 K mt in 19 years. However, a more recent survey in 2017 after recovery from the late 2000s population crash (> 600 K mt; Sydeman et al., 2020), again showed a distinct bimodal separation at 110 mm for central California CSNA (roughly Bodega Bay to Morro Bay; Zwolinski et al., 2019). Rhinoceros auklets bring in whole fish prey to their colony, which are then collected, measured and frozen, offering the opportunity for extracting anchovy otoliths in the future for ageing and comparison to length.

Extremely low samples sizes in 2010, 2011, and 2012 required dropping these years completely. Anchovy biomass estimates were also extremely low in these years (Thayer et al., 2017) and likely the cause of sparse samples; however, information on population size structure in these years might further help inform the relationships between population biomass and individual length frequencies.

4.1.1. Potential methodological biases

Our results suggest that the relative selectivity was likely to be very similar for seabirds and midwater trawls in years of high CSNA biomass (1999, 2000, 2004–2007) and when spatial extent occupied by anchovy is likely large (MacCall, 1990; Barange et al., 2009). Not surprisingly, differences between sampling methods were more apparent in years of low anchovy biomass, when anchovy become patchier and range contraction occurs. Multiple factors may be influential. Seabirds target prey patches, whereas standardized trawl sampling may not always capture very patchily-distributed fish. Indeed, during the California

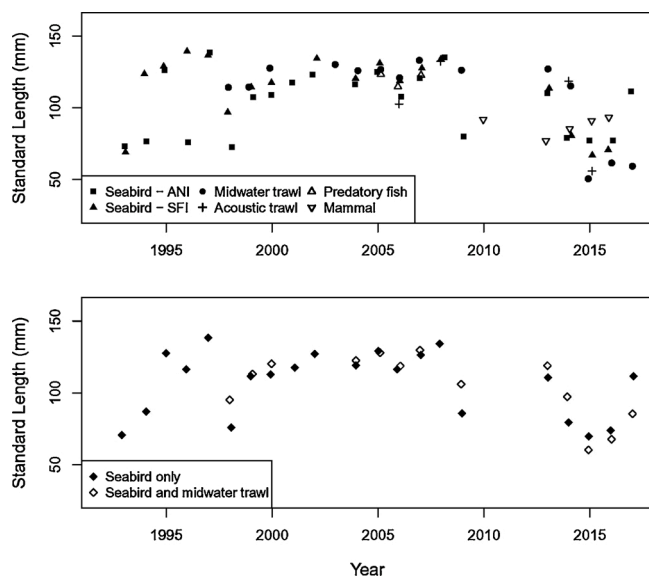


Fig. 4. Time-series of available mean anchovy length measurements (a) and the calculated Anchovy Length Indices (ALI) between 1993–2017 (b) for central California.

Department of Fish and Game Sea Survey Program for small schooling pelagic fishes (1966–1983), the degree of school formation behavior was the dominant factor behind large fluctuations in midwater trawl survey results for anchovy biomass (Mais, 1974). Additionally, patchy distribution may simply make it less likely that all sizes will be sampled, since similarly-sized fish tend to school together (Misund, 1993).

Furthermore, since anchovy growth rates can be variable from year to year (Parrish et al., 1985; Fiedler et al., 1986; Butler et al. 1989), our methodological assumption of static growth rates may not be ideal. Adjustment for the range of sampling dates was necessary, however, due to high rates of anchovy growth in the first year of life, and simple adjustments based on fixed growth rates were more easily justified from available data. Age-length relationships have shown that growth is essentially linear in the adult phase (age 1+; Parrish et al., 1985). While juvenile growth is not linear, we broke up the juvenile phase into portions and roughly assigned linear growth rates to each. Adjusting based on sampling date, however, had the effect of further separating the relative selectivity peaks of bird and trawl data in two very anomalous years, 1998 and 2009. While 1998 was a very strong ENSO year, 2009 was characterized as moderate ENSO³ with weaker than normal upwelling in the California Current System and several extended relaxation events contributing to warming during summer (Bjorkstedt et al., 2010). Anchovy growth is generally slower during ENSO conditions (Fiedler et al., 1986; Butler et al. 1989); thus, over-adjustment may have occurred in our model due to slower growth in these instances. Effects of ENSO on anchovy appear to vary, however (see Bertrand et al., 2004; Canales et al., 2016), and shifts in relative selectivity were not observed in other ENSO years during our study.

Alternatively, or perhaps concurrently, because anchovy populations contract inshore and seek spatio-temporal refuges during warm events such as ENSO (MacCall, 1990, 2009; Bertrand et al., 2004), seabirds may have better sampled very nearshore habitats where there are no trawl stations. In 1998 and 2009, seabird sample size from inshore ANI was indeed larger than from offshore SFI. A size distribution pattern of smaller fish inshore to larger fish offshore was observed in the Sea Survey (Mais, 1974), suggesting that RREAS trawls, conducted in depths of >50 m, may miss some small fish distributed very nearshore. Anchovy length distribution from the Sea Survey in central California appeared similar to the RREAS results in our study (Fig. 2b), skewed towards larger anchovy and implying under-sampling of small fish (Mais, 1974) in some years. Seabirds sampled juvenile anchovy in 1998, 2009, 2013, 2014, and to a lesser extent in 2000, when trawls did not. Although 2013, 2014 and 2000 were not ENSO years, all were relatively low biomass years (Table A3) when anchovy may have been concentrated inshore, particularly smaller fish. When more small fish were observed in trawl versus bird samples in 2015–2017, these years of initially low but increasing anchovy biomass suggest expanding across-shelf distribution and availability to trawls.

Spatio-temporally, there are potentially different distributions of anchovy in June-July during seabird sampling compared to the trawl sampling period in May-June. Whereas we adjusted for fish growth among sampling dates, we could not account for fish movement and changes in spatial distribution through time. Anchovy distribution has been associated with environmental variables such as coastal upwelling, currents, and prey availability (MacCall, 2009; Bakun et al., 2014; Canales et al., 2016; Rykaczewski et al., 2018; Benoit-Bird et al., 2019), which can change on a short time-scale. In 2014, for example, trawl sample size in May was small ($n = 19$, extrapolated $n = 38$) and clumped in southern Monterey Bay, while bird sample size in June-July was higher ($n = 71$, extrapolated $n = 86$) and spread out spatially (both ANI and SFI samples). The RREAS trawl sampling regions expanded starting in 2004 to include areas both north and south of the core area (Sakuma

et al., 2016); therefore examination of anchovy sampled by trawls outside of the core region was possible in 2014. Samples in 2014 just south of the core stations (35.7–36.6 °N) would have greatly increased sample size (to $n = 96$, extrapolated $n = 921$), and drastically changed the length frequency distribution from a mean of 115 mm in the core region, to 62 mm overall, closer to the mean anchovy length sampled by birds that year (mean = 79 mm).

Whereas birds are expected to select larger fish to maximize their return to chicks per foraging trip based on optimal foraging theory (Orians and Pearson, 1979; Ricklefs, 1985; Anthony et al., 2000), experimental trials on adult birds in the same family as rhinoceros auklets (Alcidae) did not show a prey length preference among fish up to 220 mm (larger than the maximum size anchovy captured in our study), although clupeids with smaller girth were consistently chosen (Swennen and Duiven, 1977). Gape size limits prey size in alcid; therefore, small fish prey are appropriate for small chicks, but as chicks grow and gape size and energetic requirements increase, larger fish would be expected to be selected (Bertram et al., 1991). In a given year, auklet chicks hatch over a 30–60 day period (Thayer and Sydeman, 2007), and because ANI/SFI fish sampling does not start until after peak hatch (J. Thayer unpublished data), overall sampling captures most if not all of the size spectrum of the anchovy population.

The years in this study that lacked trawl data on anchovy size, 1993–1997, were all relatively high biomass years (> 150 K mt). It is therefore likely that seabird diet samples represented the entire length frequency distribution of the local anchovy population, and that seabird data can be used as a reliable indicator of absolute anchovy size as well as inter-annual trends during this time period. In years of low anchovy biomass (< 150 K mt), the seabird index can represent inter-annual trends and indicate dominance of smaller fish in the population size distribution (< 100 mm). If of particular interest, use of mixture models for individual years could provide information on the actual mean and spread of juvenile fish sizes (see Macdonald and Pitcher, 1979; Chauvet et al., 2019).

4.2. Variability in anchovy size

Mean anchovy length and CSNA biomass varied greatly during the course of our study (from < 100 K mt to > 2 M mt; MacCall et al., 2016; Thayer et al., 2017; Sydeman et al. 2020), which included numerous anomalous oceanographic conditions. An extreme La Niña event of cool ocean conditions and intense upwelling characterized 1999 and stretched into 2000 (Chavez et al., 1999). Warm conditions prevailed in multiple years, with ENSO events in 1997–1998, 2004, 2009–2010, and 2015–2016⁴. Unusual atmospheric blocking in the Gulf of Alaska in spring 2005 resulted in poor upwelling-favorable winds and anomalously warm sea surface temperatures in the California Current (Sydeman et al. 2006) and substantially delayed the onset of upwelling through 2006 (Schwing et al., 2006; Goericke et al., 2007). There was an unprecedented marine heat wave in 2015 (“The Blob”; Bond et al., 2015; Gentemann et al., 2017). Most recently, 2017 was the warmest year on record without an ENSO event in the tropical Pacific Ocean⁴.

Inter-annual variability in fish size reflects changes in population structure and year class strength, an important consideration for understanding recruitment and changes in population size. In the current study, anchovy cohorts as sampled by midwater trawls and seabird diets are evident through time (Fig. 2a). Small mean anchovy lengths were associated with ENSO events (Linear regression with Oceanic Niño Index: $R^2 = 0.43$, $p = 0.04$; similar to findings of Fiedler et al., 1986). During the warm period in 2015, high levels of anchovy larvae were observed throughout California Current waters for prolonged periods

³ https://www.cpc.ncep.noaa.gov/products/analysis_monitoring/ensostuff/ensoyears.shtml

⁴ NOAA National Centers for Environmental Information (2018) State of the Climate: Global Climate Report for Annual 2017. <https://www.ncdc.noaa.gov/sotc/global/201713>.

(this study, Sakuma et al., 2016; Auth et al., 2017, NMFS SaKe survey⁵). Substantial recruitment from age 0 to age 1 was not evident during the anchovy population crash (2009–2015; Sakuma et al., 2017), Zwolinski et al., 2016). More age 1+ fish were evident in 2016 in southern California (Sakuma et al., 2017); fish of sizes corresponding to age 1 (~110 mm in summer) were predominant from southern to central California (Zwolinski et al., 2017), and the successful recruitment of this 2015 cohort appears largely responsible for the anchovy population recovery in 2017–2018 (Zwolinski et al., 2019; Thayer et al., 2017; Sydeman et al., 2020; Table A3). As lengths of time-series increase, incorporation of other non-traditional data sources such as predatory fish and/or pinniped diet could be examined to potentially increase robustness of the anchovy length indicators (see Mills et al., 2007). Additionally, future development of non-traditional indicators in southern California (sea lions and seabirds) will help to provide a more complete picture of anchovy length frequencies throughout the CSNA range.

In the longer term, such information can be useful for better understanding population dynamics of both predators and prey from a more holistic perspective. This can be done from both the perspective of single species stock assessments, for which data from predators may serve to inform trends in recruitment, age structure, abundance, and potentially shifts in predation mortality rates for forage species (Tyrrell et al., 2011; Johnson et al., 2015). Another approach is from the perspective of harvest strategy development, in which availability of forage to predators is explicitly accounted for in the setting of harvest control rules (Punt et al., 2016; Holsman et al., 2016). Moreover, data and insights regarding predator dynamics and selectivity are critical to long term improvements in ecosystem models, as such data are key to modeling the spatial and temporal shifts in predation by higher trophic level predators, and ultimately to informing parameterization of functional relationships between predators and prey (e.g., Kinsey and Punt, 2009, Hunsicker et al., 2011). Ultimately, management will be best informed by ecosystem models that are capable of replicating the predator-prey dynamics that are inferred by empirical data collections, a considerable challenge for high turnover species such as northern anchovy, but critical to long-term efforts to most effectively balance the trade-offs between fisheries and predators in the context of a volatile population and highly dynamic environment.

CRedit authorship contribution statement

J.A. Thayer: Conceptualization, Methodology, Data curation, Writing - original draft, Supervision, Funding acquisition. **Z. Burr:** Methodology, Software, Formal analysis, Visualization. **J. Field:** Data curation, Methodology, Writing - review & editing. **R.D. Carle:** Data curation, Writing - review & editing. **P. Warzybok:** Data curation.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.fishres.2020.105801>.

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⁵ http://www.pcouncil.org/wp-content/uploads/2016/11/G4a_Sup_SWFSC_Rpt2_NOV2016BB.pdf

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