

CORRECTING FOR BIAS IN CALCOFI ICHTHYOPLANKTON ABUNDANCE ESTIMATES ASSOCIATED WITH THE 1977 TRANSITION FROM RING TO BONGO NET SAMPLING

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ABSTRACT

To correctly interpret trends in species' abundance in long time series it is essential to account and correct for biases that may arise in association with changes in sampling methodology. We assess how gear changes for oblique plankton net tows (from 1 m diameter ring to 0.71 m diameter bongo net in 1977) affected ichthyoplankton abundance estimates from the California Cooperative Oceanic Fisheries Investigations (CalCOFI) program. Paired ring and bongo net samples were analyzed from 133 stations sampled in 1977–78. To quantitatively correct for net-associated bias, we first modeled abundance in bongo nets as a function of abundance in ring nets for larvae and eggs summed across all taxa during day and night with generalized linear models (GLM; identity link with gamma error structure). Models suggest that greater visual avoidance for ring than bongo nets induces bias in abundance estimates as slope estimates were greater than 1 for combined larvae during the day but did not differ significantly from 1 for combined larvae at night, or eggs during day or night. Ratios of summed abundances between bongo and ring nets for the 15 most common taxa indicated that there were significantly higher abundances for 4 taxa in the bongo than the ring net during the day but values did not differ at night between net types. To make data collected in ring nets before 1978 more comparable to data from bongo nets our results suggest it is necessary to adjust abundance estimates during the day from ring nets by a factor of 2 for *Cyclothone* spp., 2.17 for *Diogenichthys* spp., 2.06 for *Engraulis mordax*, and 1.53 for *Vinciguerria* spp. It may also be necessary to reevaluate results from past studies that utilize the CalCOFI larval time series that did not correct for net bias. More data are needed to ascertain the effect of net change on species such as *Sardinops sagax* or *Tarletonbeania crenularis* that were uncommon in the late 1970s but have been encountered frequently in recent years.

INTRODUCTION

Long time series are essential for truly understanding the mechanisms governing variability in the dynamics of populations and communities in all ecosystems

(Krebs et al. 2001; McClatchie 2014). Short-term fluctuations are often nested within long-period dynamics and attempts to discern the causes of species variability over short time periods may produce erroneous conclusions (McClatchie et al. 2017). This is particularly true in an era of rapid climate change as the effect of changes in environmental conditions on ecosystems can be conceptualized only when placed in the context of a long time series. Therefore, it is extremely important for species management and conservation programs to maintain and build upon long time series over upcoming years and decades.

Equally important as maintaining long time series is ensuring that samples collected over time are comparable to one another. Bias can arise if systematic differences in collection methods that affect the probability of capturing an organism are imposed upon the time series (MacKenzie et al. 2002). For example, trends from fishery-dependent data may not reflect true population dynamics of a fished species if the fleet introduced more effective gear for catching the targeted species at some point in the time series. Accounting for methodological differences in data collection is imperative to properly interpret potential changes in species abundances for time series analysis (MacKenzie et al. 2005).

The California Cooperative Oceanic Fisheries Investigations (CalCOFI) program provides some of the most complete marine ecosystem monitoring data in the world. CalCOFI has continuously sampled biological (plankton tows) and oceanographic conditions (CTD and water collections) from the same 66 core stations off southern California since 1951 (McClatchie 2014). From a biological perspective, the resultant data give information on variability in the distribution and abundance of zooplankton (McGowan and Walker 1985; McGowan et al. 1998; Lavaniegos and Ohman 2007) and ichthyoplankton (Hsieh et al. 2005; Hsieh et al. 2006; Hsieh et al. 2009; Lindegren et al. 2016) over more than six decades.

At several points in the time series CalCOFI plankton sampling was changed to introduce methodological improvements. In all years, samples were obtained by lowering a net to a set depth and towing it obliquely (at a 45° angle) to the surface at a constant speed. However,

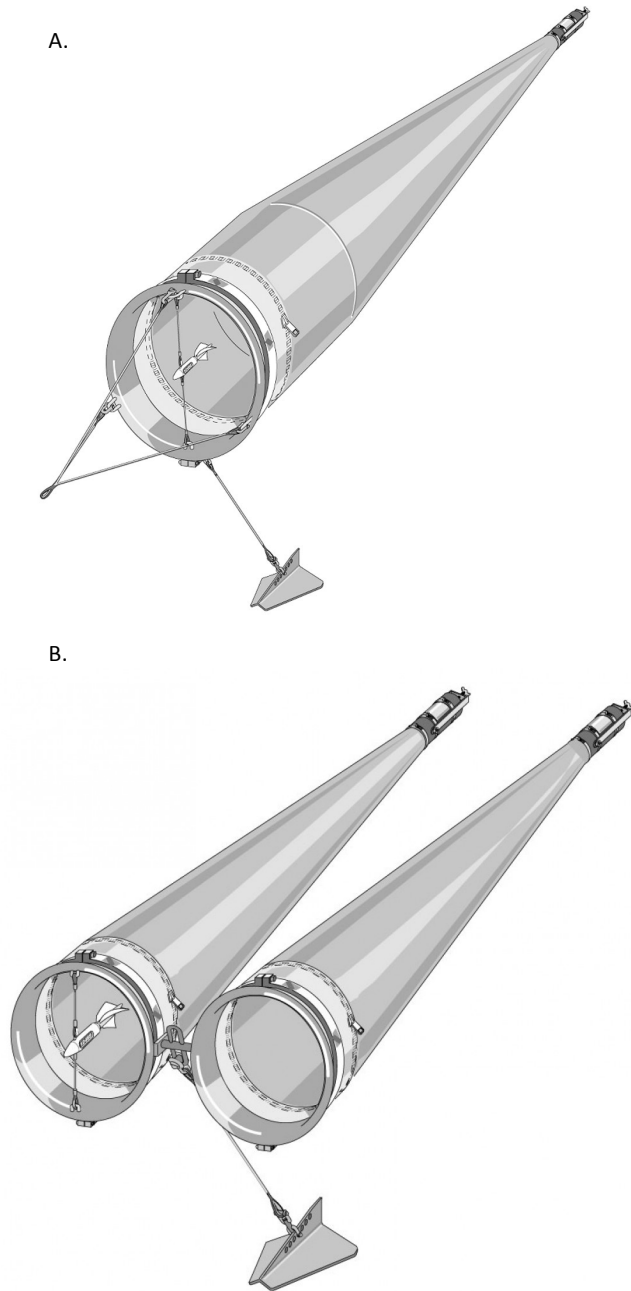


Figure 1. Illustrations of A. ring and B. bongo nets. Note that the bridle is directly in front of the mouth of the ring net but connects to the frame between the twin nets of the bongo, leaving the net mouths unobstructed (samples analyzed here were taken from the starboard net). Illustrations kindly provided by Hydro-Bios (<http://www.hydrobios.de>).

different types of nets were used at various time periods. From 1951 to fall 1977 plankton were collected using a ring net with a 1 m diameter mouth (fig. 1). Due to concern that the ring net bridle (fig. 1A) diminished zooplankton sampling efficiency, bongo nets that have an offset bridle (fig. 1B) (McGowan and Brown 1966) were introduced in the winter of 1977. To deduce how these two nets affected collection efficiency, samples were col-

lected using both nets at the same 160 stations during seven CalCOFI cruises between winter 1977 and summer 1978. At present, net effects on sampling efficiency have been thoroughly vetted for zooplankton (Smith 1974; Brinton and Townsend 1981; Ohman and Smith 1995; Rebstock 2001; Ohman and Lavaniegos 2002). However, with the exception of an investigation on northern anchovy, *Engraulis mordax* (Hewitt 1980), comparable analyses have not been published for ichthyoplankton. Here we evaluate if larval abundance estimates are biased by gear type and test the hypothesis that bias will be greater during the day when larvae would be able to better see and avoid the ring than the bongo net.

METHODS

Collection

One hundred and sixty paired ring and bongo samples were taken during seven CalCOFI cruises (7712, 7801, 7803, 7804, 7805, 7807, and 7808) in 1977 and 1978. The sampling area varied somewhat by cruise but overall ranged from just north of Monterey Bay, California, to offshore of Bahia de Magdalena, Baja California Sur (fig. 2). The majority of samples were collected at CalCOFI station 60, which is located over the continental slope. Additional sample sites were closer inshore between CalCOFI station 30 and 40 (mostly at 30) and further offshore at station 90.

Ring and bongo nets had 1 and 0.71 m diameter mouth openings, respectively, and 0.505 mm mesh. Both were towed obliquely (approximately 45°) from 210 m to the surface following standard CalCOFI methodology (Kramer et al. 1972; McClatchie 2014). Samples were collected during both night and day and paired samples were typically obtained within 30 minutes of each other. Plankton from the starboard side of the bongo (samples were not collected on the port side as there wasn't a cod end attached to the port net) and from the ring net were preserved in sodium borate-buffered 2% formaldehyde at sea. We included samples collected less than half an hour before sunrise or after sunset in the day samples because there is still typically some light during this period.

Fish eggs and larvae were sorted from the plankton and identified to the lowest practical taxon at the NOAA Southwest Fisheries Science Center ichthyoplankton laboratory. Larval identification was conducted for 133 of the 160 stations where paired samples were collected from cruises 7712, 7801, 7803, 7804, 7805, and 7807 (fig. 2). Subsampling (usually 50%) was done prior to sorting if zooplankton abundances were excessively high. Most taxa were identified to species, but some were characterized to genus (bristlemouths, *Cyclothone*; sanddabs, *Citharichthys*; lampfishes, *Nannobranchium*; rockfishes, *Sebastes*; and lightfishes, *Vinciguerria*). To standard-

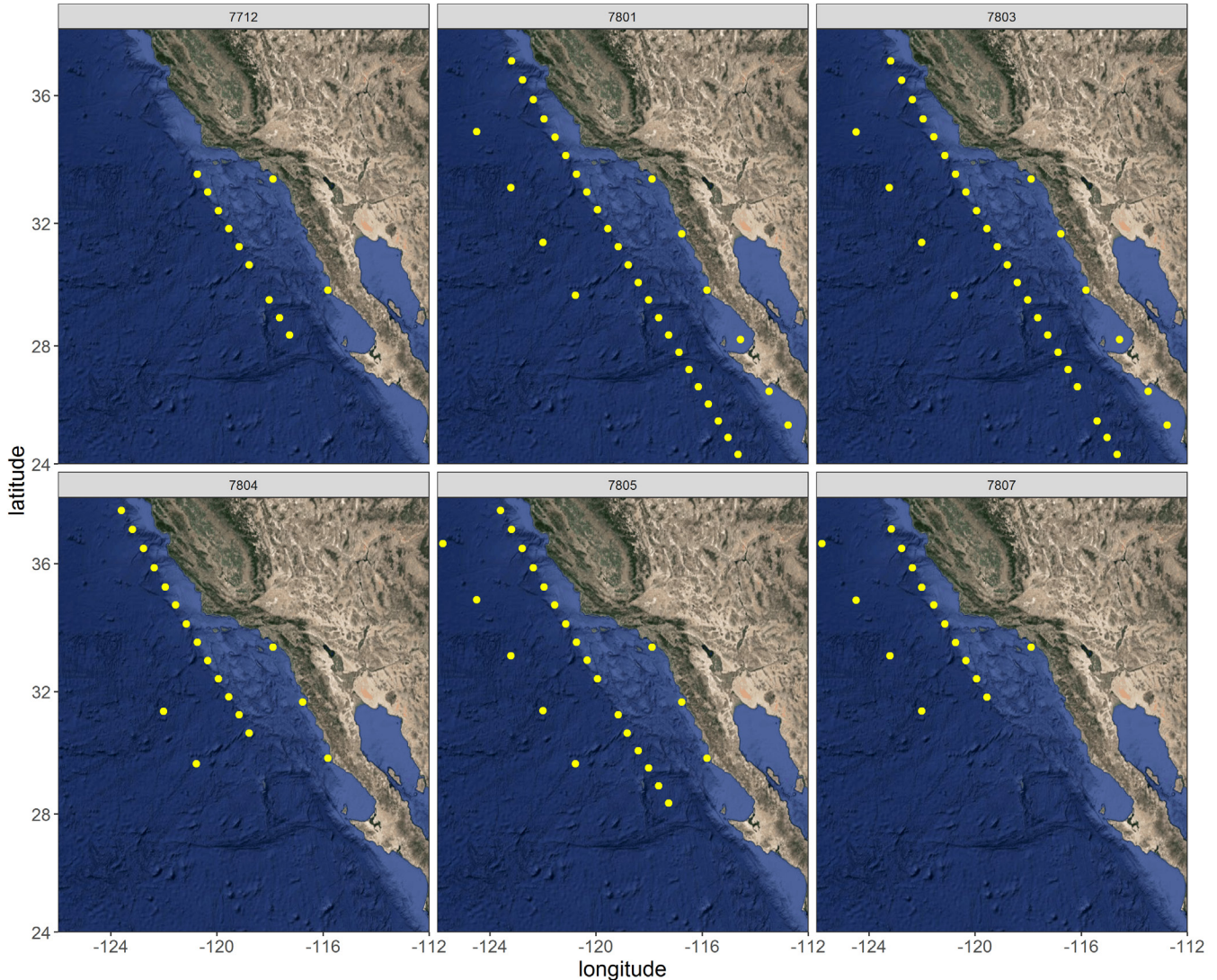


Figure 2. Sampling locations in each of 6 cruises. The first two digits of the cruise name is the year (i.e., 1977 and 1978) and the last two digits are the month.

ize differences in the amount of water filtered or tow depths, raw larval counts were divided by the proportion of the sample that was sorted and multiplied by a standard haul factor based on flowmeter data (Kramer et al. 1972; McClatchie 2014) such that final abundances were expressed as individuals under 10 m² of sea surface.

Analysis

We began by modeling the pooled abundance of all larval taxa in bongo nets as a function of the pooled abundance of all larval taxa in ring nets for paired samples to determine if there was evidence for differences in the efficiency of larval capture between net types. Our working hypothesis was that larvae may visually avoid the bridle in front of the ring net and that this effect would manifest during the day but not at night. We therefore tested bongo~ring relationships separately

for samples collected during day and night. We further assessed the potential for visual avoidance by modeling fish eggs in the bongo versus ring nets. Because eggs are passive particles we hypothesized that there would be no difference in egg abundance between nets, for both day and night collections.

We modeled the relationship between paired bongo and ring abundances for each species group and day/night category using generalized linear models (GLMs). Preliminary exploration of the data indicated that the variability in bongo abundance increased with increasing abundance, and model residuals using several distributions and link functions suggested that model assumptions were best met using a gamma distribution with an identity link function.

If the slope of the bongo~ring relationship did not differ from 1, then there would be no difference in

TABLE 1
 Estimated species-specific ratios of summed abundances and 95% confidence for the 15 most abundance species, for daytime and nighttime samples. “No. stations” refers to the number of stations where the species was present (out of 133 stations). Confidence intervals that do not overlap with 1 are shown in bold font.

| species | no. stations | day/night | bongo/ring ratio | 2.5% CI bound | 97.5% CI bound |
|-----------------------------------|--------------|-----------|------------------|---------------|----------------|
| <i>Bathylagoides wesethi</i> | 22 | day | 1.23 | 0.66 | 1.80 |
| <i>Citharichthys</i> spp. | 20 | day | 1.29 | 0.63 | 1.94 |
| <i>Cyclothone</i> spp. | 31 | day | 2.00 | 1.21 | 2.79 |
| <i>Diogenichthys</i> spp. | 32 | day | 2.17 | 1.42 | 2.92 |
| <i>Engraulis mordax</i> | 17 | day | 2.06 | 1.57 | 2.56 |
| <i>Leuroglossus stilbius</i> | 11 | day | 1.66 | -0.52 | 3.83 |
| <i>Lipolagus ochotensis</i> | 37 | day | 1.55 | 0.87 | 2.23 |
| <i>Merluccius productus</i> | 21 | day | 2.04 | 0.42 | 3.66 |
| <i>Nannobranchium</i> spp. | 40 | day | 1.48 | 0.88 | 2.08 |
| <i>Protomyctophum crockeri</i> | 39 | day | 1.45 | 0.75 | 2.14 |
| <i>Sebastes</i> spp. | 30 | day | 1.18 | 0.81 | 1.55 |
| <i>Stenobranchius leucopsarus</i> | 28 | day | 1.79 | 1.01 | 2.57 |
| <i>Trachurus symmetricus</i> | 19 | day | 1.38 | 0.84 | 1.91 |
| <i>Triphoturus mexicanus</i> | 24 | day | 2.53 | 0.95 | 4.11 |
| <i>Vinciguerria</i> spp. | 32 | day | 1.53 | 1.01 | 2.04 |
| <i>Bathylagoides wesethi</i> | 22 | night | 0.82 | 0.60 | 1.04 |
| <i>Citharichthys</i> spp. | 36 | night | 1.36 | 0.82 | 1.89 |
| <i>Cyclothone</i> spp. | 21 | night | 1.44 | 0.80 | 2.08 |
| <i>Diogenichthys</i> spp. | 26 | night | 0.98 | 0.55 | 1.42 |
| <i>Engraulis mordax</i> | 28 | night | 1.16 | 0.98 | 1.35 |
| <i>Leuroglossus stilbius</i> | 23 | night | 1.14 | 0.87 | 1.42 |
| <i>Lipolagus ochotensis</i> | 35 | night | 0.98 | 0.65 | 1.31 |
| <i>Merluccius productus</i> | 24 | night | 1.16 | 1.01 | 1.32 |
| <i>Nannobranchium</i> spp. | 31 | night | 1.00 | 0.46 | 1.55 |
| <i>Protomyctophum crockeri</i> | 37 | night | 0.94 | 0.61 | 1.27 |
| <i>Sebastes</i> spp. | 29 | night | 0.96 | 0.64 | 1.28 |
| <i>Stenobranchius leucopsarus</i> | 29 | night | 1.40 | 0.99 | 1.82 |
| <i>Trachurus symmetricus</i> | 19 | night | 1.47 | 0.57 | 2.37 |
| <i>Triphoturus mexicanus</i> | 13 | night | 0.82 | 0.55 | 1.08 |
| <i>Vinciguerria</i> spp. | 22 | night | 0.85 | 0.59 | 1.11 |

abundance estimates between the two nets and hence no need to make adjustments to abundance estimates. Therefore, we evaluated whether estimated slopes from daytime and nighttime data differed significantly from 1 using t-tests: (t-statistic = (slope estimate-1)/(slope standard error) with the degrees of freedom equal to the number of observations - 2, and measuring significance based on a one-tail t-distribution (Zar 1996).

We next explored how net bias affected individual taxa as model results revealed that summed larval abundances, pooled over taxa, were greater in the bongo than ring nets during the day. We limited taxa-specific analyses to the 15 taxa that were found in at least 10 stations during both day and night (table 1). Model diagnostics indicated that GLMs fitted to the individual species data performed poorly, even when using hurdle and zero-inflated models. Hence, we examined the ratio of the sum of abundance from the bongo net to the sum of abundance from the ring net, for each of the 15 taxa, day and night, where the sums were computed across all stations. We calculated approximate 95% confidence intervals (CI) analytically for each of these ratios using the methods outlined in Levy and Lemeshow (2008) and considered ratios significantly different from 1.0 if

the CI did not contain the value 1. Ratios of sums have the potential to be unduly influenced by small number of samples with high abundances. Therefore, to test the sensitivity of the species-specific ratio estimates to a relatively few number of samples with very high abundances, we sorted all pairs by samples based on abundance in the bongo net and sequentially trimmed the lowest and highest abundance stations, from 1% to 10%, and calculated ratios and 95% CI at each level of trimmed data.

If active avoidance was the cause of net bias, then smaller, weaker swimming larvae would be less likely to exhibit net bias than larger, relatively well developed individuals. Larval sizes were available for northern anchovy, *Engraulis mordax*, and Pacific hake, *Merluccius productus*. We created size bins for anchovy that were similar to Hewitt (1980) who also evaluated differences in catch ratio between ring and bongo nets. Because the number of larvae was sparse at larger sizes we grouped sizes between 7.25 and 31 mm so that abundances exceeded 100 individuals for each bin during day and night. For hake, bin size classes were created so that at least 100 individuals fell within each bin. We then calculated ratios of sums and 95% CIs for each bin and determined if the CI overlapped 1.

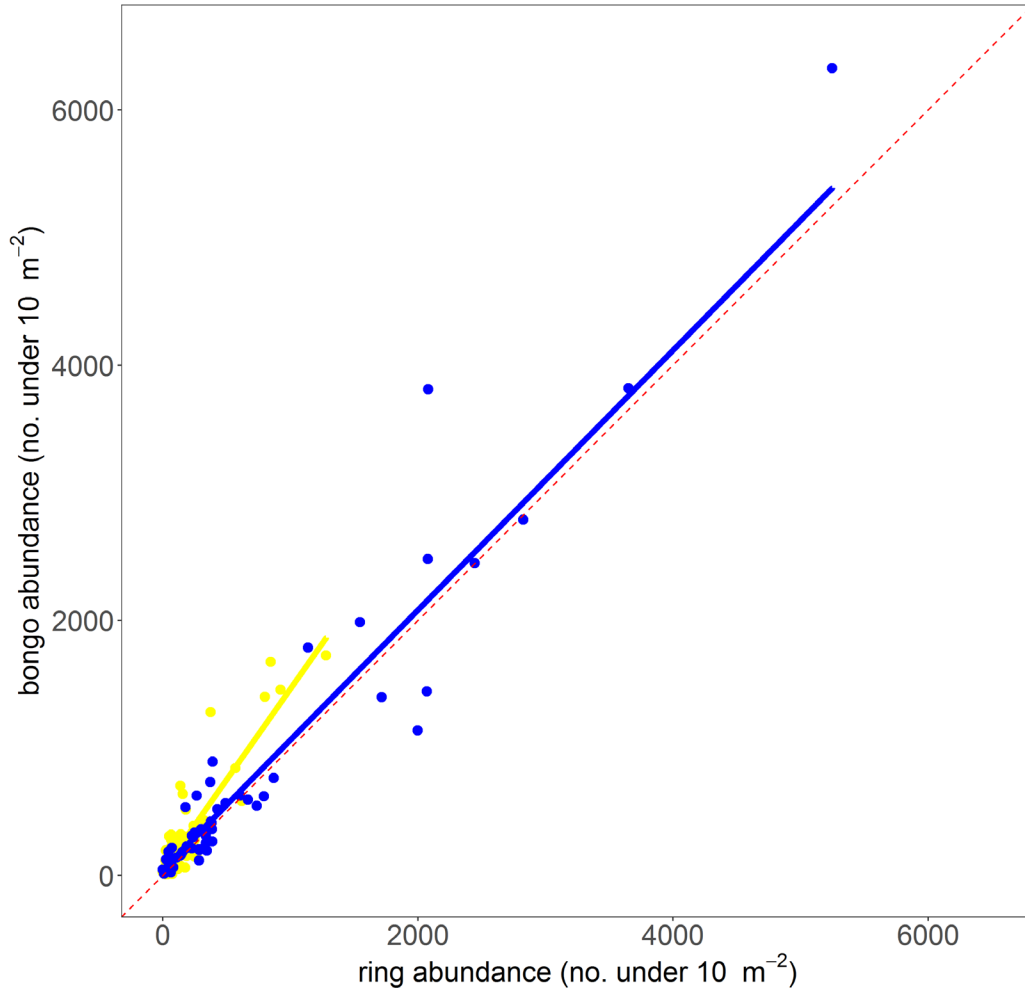


Figure 3. Scatter plot of paired abundances (all taxa) from ring and bongo nets at each station. Blue depicts samples taken at night while yellow characterizes samples collected during the day. Solid lines show the estimated linear relationships from the gamma models.

All analyses were conducted using the R statistical software. GLMs were fitted using the “glm” function in the R software environment version 3.2.3 (R Core Team 2015). The R package StreamMetabolism version 1.1.1 (Sefick Jr. 2015) determined whether it was day or night based on the date, time, latitude and longitude of a station. We used the package survey version 3.31–2 (Lumley 2016) to calculate 95% CI around ratios of summed abundances. All plots were created using ggplot2 version 2.1.0 (Wickham 2009) and/or ggmap version 2.6.1 (Kahle and Wickham 2013).

RESULTS

The estimated slope of the relationship between ring and bongo abundances of pooled larval taxa was significantly different from 1 for daytime samples (fig. 3; $\text{bongo.abundance} = 1.42 \cdot \text{ring.abundance} + 39.7$; intercept s.e. = 12.6, slope s.e. = 0.19; test of H_0 : slope = 1: $t = -2.27$, $p = 0.026$). Estimated slopes did not differ from

1 for pooled larval taxa from nighttime samples (fig. 3; $\text{bongo.abundance} = 1.02 \cdot \text{ring.abundance} + 45.2$ slope s.e.=0.087, test of H_0 : slope = 1: $t = -.21$, $p = .83$) or for eggs from either daytime ($\text{bongo.abundance} = 0.89 \cdot \text{ring.abundance} + 20.3$; intercept s.e. = 9.51, slope s.e. = 0.19; test of H_0 : slope = 1: $t = 1.1$, $p = 0.26$) or nighttime samples ($\text{bongo.abundance} = 1.02 \cdot \text{ring.abundance} + 13.2$; intercept s.e. = 13.3, slope s.e. = 0.11; test of H_0 : slope = 1: $t = -.15$, $p = 0.88$).

Species-specific estimated ratios of summed abundances (bongo/ring) from daytime samples were significantly greater than 1 for one-third of the most common taxa: *Cyclothone* spp., *Diogenichthys* spp., *Engraulis mordax*, *Stenobranchius leucopsarus*, and *Vinciguerria* spp. (table 1, fig. 4). For 4 of these 5 taxa, sensitivity analyses suggested that there was no strong evidence that the ratio estimates were unduly affected by outliers; ratio estimates were significantly greater than 1 on most or all of the trimmed data sets (fig. 5). *Stenobranchius leucopsarus*

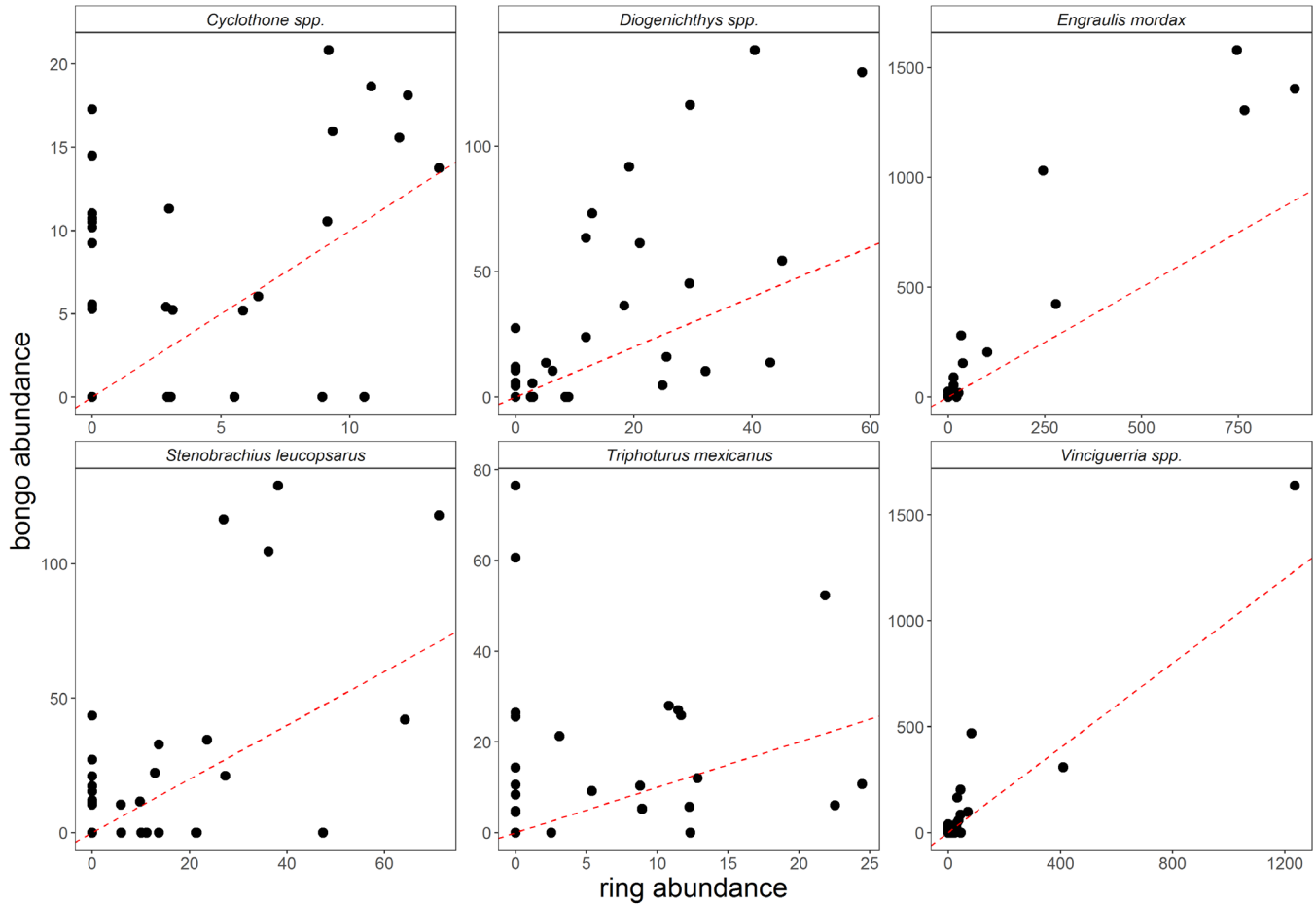


Figure 4. Scatter plots of species-specific abundances from paired ring and bongo daytime samples for the five species with estimated ratios of summed abundances significantly greater than 1. Diagonal red, dashed lines depict 1:1 relationships. Note that scales differ on x and y axes.

rus, however, was affected by trimming as removal of the lowest and highest 1% and 6%–10% resulted in confidence intervals that overlapped 1. Similarly, for most of the ten taxa with ratio estimates not differing significantly from 1, trimming did not lead to estimates that were consistently different from 1. The one exception was *Triphoturus mexicanus* where the trimmed data sets at 1%–4% and 6%–8% had estimated slopes greater than 1.

In contrast to the daytime results, 95% confidence intervals for the species-specific ratios of summed abundances overlapped 1 for all taxa except *Merluccius productus* (table 1). The ratio estimate for *Merluccius productus*, however, was sensitive to data trimming as ratios from only half of the trimmed data sets were significantly greater than 1.

Estimated bongo/ring ratios were significantly greater than 1 for *Engraulis mordax* at all but the smallest size bin for daytime samples (fig. 6). Nonetheless, there was a tendency for variance about the ratio estimates to increase with size, and the 95% CI for the largest size

bin completely contained the 95% CIs for two of the three smaller size bins suggesting that there was no significant difference in the ratio as a function of size. For nighttime samples, CIs of the estimated ratios for 3 of the 4 size bins overlapped 1. Ratios did not differ significantly from 1 for *Merluccius productus* at any size bin for daytime samples and there was no indication that the daytime ratio changed with size. At night, the 95% CI around the ratio for *Merluccius productus* were below 1 for the smallest size class but did not differ from 1 for the other size classes.

DISCUSSION

Our results indicated that the slope of bongo~ring abundance relationship was significantly greater than 1 for combined larval taxa from daytime samples but not from nighttime samples. Estimated species-specific bongo to ring ratios also were significantly greater than 1 and resilient to sensitivity analyses for 4 of the 15 most common taxa. These results indicate that adjustments need to be made to abundance estimates for *Cyclothone*

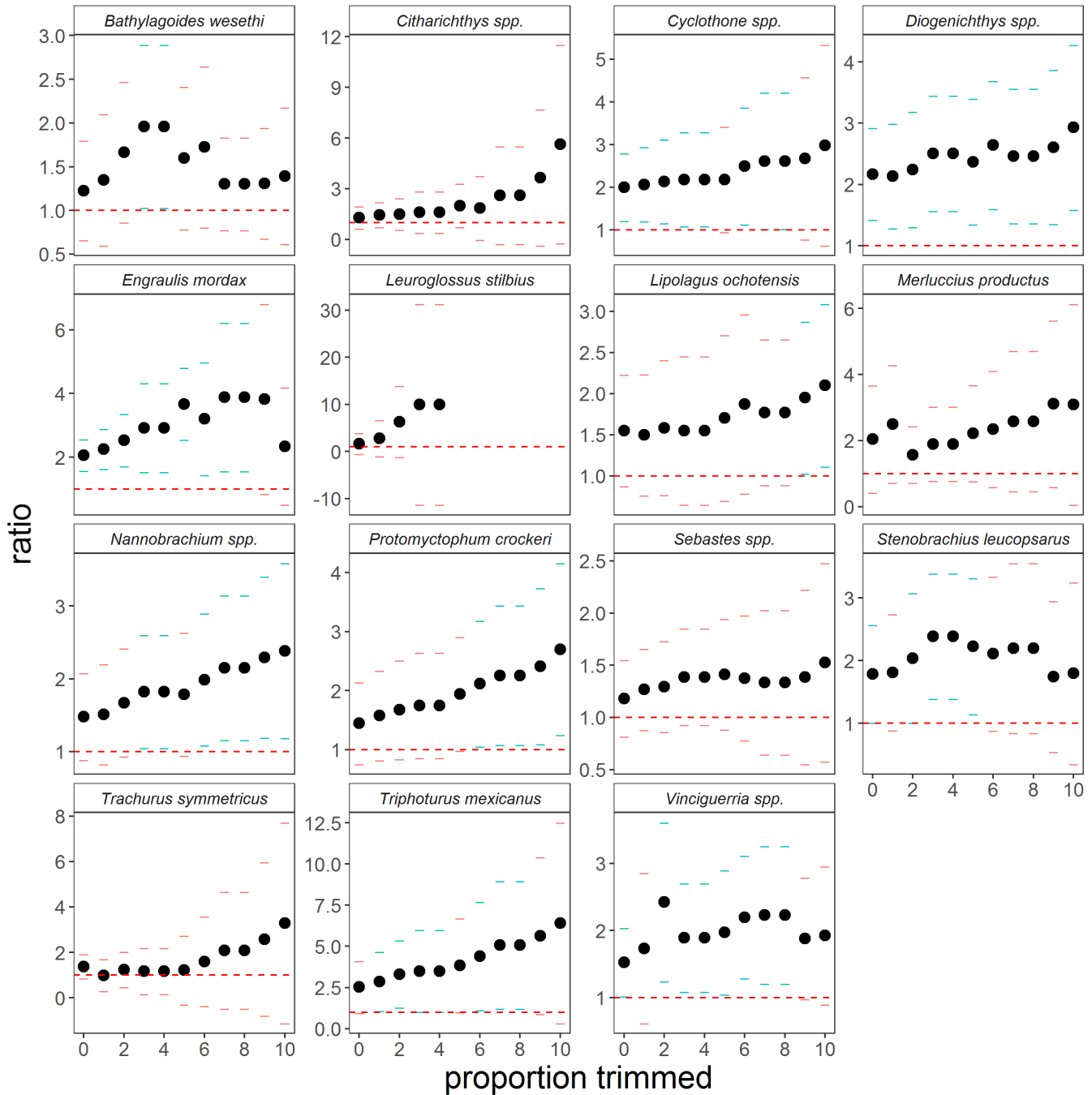


Figure 5. Estimated species-specific ratios of summed abundance and approximate 95% CIs for trimmed data sets. Horizontal, red, dashed lines depict ratios of 1. Dashes around points are 95% confidence intervals (CI). Dashes are blue if the CI does not overlap 1 and red if the CI does overlap 1.

spp., *Diogenichthys* spp., *Engraulis mordax*, and *Vinciguerria* spp. collected in ring nets prior to 1978 to ensure that the CalCOFI time series is more comparable before and after the implementation of bongo net sampling.

This is the first comprehensive analysis evaluating how changing gear affected abundance estimates of ichthyoplankton for multiple species in the CalCOFI program. Hewitt (1980), however, used these same data to

examine the relationship between bongo and ring net catches on *Engraulis mordax* larva and concluded that there was very little difference in catchability between net types. Specifically, Hewitt (1980) calculated the ratio of *E. mordax* larvae abundance at night divided by abundance at day for 15 size bins from ring and bongo nets. He concluded that there was not a large (twice as many) difference in night/day ratios between ring and bongo

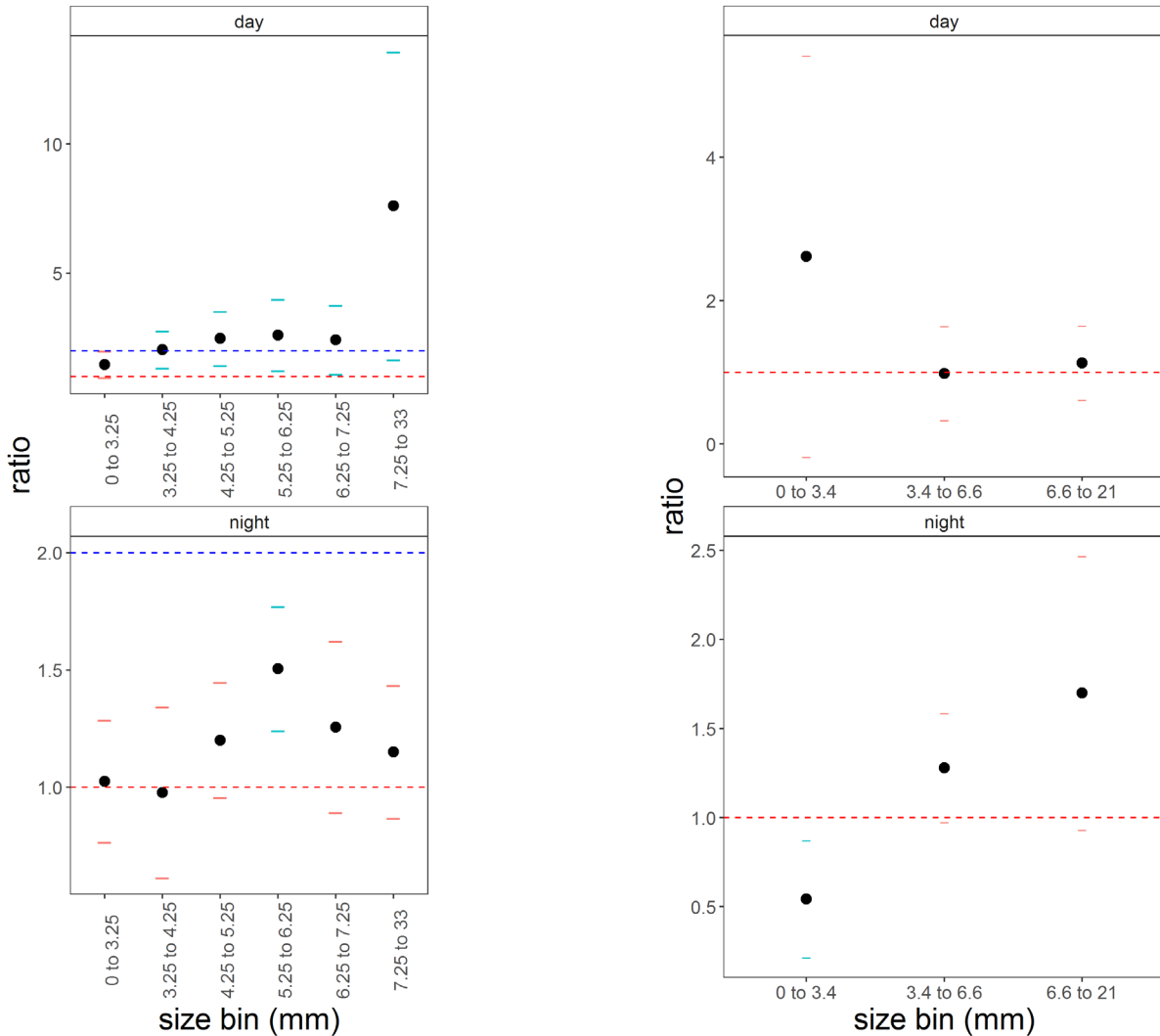


Figure 6. Estimated ratios of summed abundance by size category, and approximate 95% CIs, from daytime and nighttime samples for anchovy (*Engraulis mordax*) (top two panels) and hake (*Merluccius productus*) (bottom two panels). Bin boundaries were created so that the number of larvae were similar between bins. Dashes around points are 95% CI. Blue and red CI are those that do not and do overlap with 1, respectively. Red dashed lines are at 1 and the blue dashed line is at 2.

nets until larvae were larger than 6.75 mm and that because larvae > 6.75 mm comprised only 10% of the catch, there was no reason to correct for net bias.

Our conclusion that there is a significant difference in catchability of *E. mordax* between nets during the day likely differs from Hewitt (1980) for at least two non-mutually exclusive reasons. First, the data used in both studies was designed to test for ring/bongo rather than day/night differences. Whereas both ring and bongo samples were collected at the same stations, day and night samples were taken from different stations. Therefore, the analysis of pooled daytime *versus* nighttime samples of Hewitt (1980) would not have as effectively controlled for any overall differences in size composition among stations, as compared to the approach presented herein, where the ratios summed abundances were compared

to the value 1, for daytime and nighttime samples, separately. Second, Hewitt states that the night/day catch ratio wasn't much different between ring and bongo nets until larvae are larger than 6.75 mm. However, his interpretation of a significant difference is qualitative, and rather liberal as corrections may be necessary even if difference in ratios are less than 2. It is evident from Figure 1 in Hewitt (1980) that although the magnitude of night/day ratios between nets was reduced for larvae that were smaller than 6.75 mm, the ratio was still higher in ring nets at the smaller size classes. As Hewitt (1980) does not statistically evaluate whether the ratios differ at any size class and does not report variance associated with ratio estimates, it is possible that differences were statistically significant at smaller size classes. Indeed, we found that bongo/ring 95% confidence intervals did not

overlap with 1 during the day for all except the 0–3.25 mm size bin. Further, the confidence intervals for all except the smallest size bin overlapped Hewitt's threshold of 2. Given that 67% of anchovy larvae examined in this study (combined ring and bongo) were larger than 3 mm, it is necessary to adjust anchovy abundances collected in ring nets to make abundance estimates directly comparable before and after 1977.

Our results indicate that net avoidance is affected by whether samples were collected during the day or night. This finding, coupled with a lack of day/night effect on passive eggs and no significant ratios above 1 for any taxa at night, suggests that larvae are using visual cues to better avoid the ring than the bongo net. The importance of sample time was also shown by Hewitt (1980) as night/day catch ratios of northern anchovy larvae were close to 1 for small larvae but around to 20:1 for larger individuals. Similarly, we detected an increase in ratio with *E. mordax* size, suggesting that larger larvae that are competent swimmers are better at net avoidance than smaller individuals. Our analysis, however, showed that even small *E. mordax* avoid the ring net at a higher rate than the bongo net.

Sakuma et al. (2007) provide further evidence that larval fishes can use visual cues to avoid plankton nets. They conducted bongo net sampling from a fixed location in central California every 2 hours over consecutive days and found that larval *Sebastes* spp. were much more abundant during the night than day. Sakuma et al. (2007) ascribed this discrepancy to visual avoidance during the day as *Sebastes* spp. larvae do not undergo diel vertical migration (Sakuma et al. 1999). Although we also observed that *Sebastes* spp. summed abundances were 1.8 times higher during the night than day, the ratio of summed abundances was not significantly different from 1 for either daytime or nighttime samples (this analysis was not reported in the Results). It is possible that the visual cues generated by the two net types were too subtle to evoke a degrees of avoidance behavior for *Sebastes* spp. that we could detect with our data.

An important finding of our work is that net avoidance capabilities differed among taxa. Sakuma et al. (2007) also echoed this conclusion as they found differences in catch rates between day and night for *Sebastes* spp. but not *M. productus* in central California. One explanation for the differences in avoidance behavior among taxa may be that different taxa have inherent differences in swimming ability. There are no obvious morphological characteristics, however, that can predict which taxa may be stronger swimmers. For example, *Sebastes* spp. and *M. productus* are morphologically similar as larvae and can be mistaken for one another. Similarly, *B. wesethi* and *E. mordax* larvae both have long, slender bodies but bongo/ring ratios were very different for the

two species. More research on larval swimming behavior will need to be conducted to determine if this factor can explain variability in net avoidance. Another explanation for the differences in ratio estimates among taxa may simply be that the taxa with higher bongo/net ratios in our study had proportionally greater numbers of large individuals in the samples. Although individual sizes were only available for *E. mordax* and *M. productus* flexion stage (preflexion, flexion, and postflexion) for other taxa were recorded on data sheets. However, perusal of the raw data sheets did not indicate any systematic differences in flexion stage among taxa. A third possibility is that vertical distributions differ between taxa during the day. If some taxa reside primarily in deeper water then light will be more limited even during the day, thus impeding capacity to visually detect the net. Further research is needed to discern the precise mechanism governing the apparent variation in net avoidance capabilities among taxa.

The correction factors presented in our research are intended to be applied to abundance estimates over an entire cruise rather than at any specific station. Making corrections to individual stations is more difficult because in any given cruise a majority of stations will have 0 individuals for a given taxa. To estimate whether individuals are likely to be present when not detected will require spatial modeling of abundance or modeling of abundances as a function of environmental covariates. Most of the past studies that explored dynamics of CalCOFI ichthyoplankton (Moser et al. 2000; Moser et al. 2001; Hsieh et al. 2005; Hsieh et al. 2006; Anderson et al. 2008; Hsieh et al. 2009) evaluated abundances at an annual scale (pooled over space) and are thus directly amenable to our corrections.

Previous work comparing zooplankton from the same samples analyzed here also detected significant differences between bongo and ring nets. Analysis of 12 euphausiid species revealed that larvae were more abundant in ring nets, that juveniles and adults were more abundant in bongo nets, and that total numbers were similar between nets (Brinton and Townsend 1981). Ohman and Smith (1995) found that overall zooplankton biomass was 1.36 times higher in bongo than ring nets. A follow up to this study showed that zooplankton differences among nets were driven primarily by salps (2.68 times more abundant in bongo nets) and secondarily by pteropods (1.09 times more abundant in bongo nets) while 15 other categories of zooplankton did not differ between net types (Ohman and Lavaniegos 2002). It thus appears that fish larvae abundance estimates were more affected by the transition from ring to bongo sampling than most zooplankton species.

Optimizing plankton sampling is a methodological challenge to fisheries science, and studies from around the globe have documented how gear affects ichthyo-

plankton abundance estimates. For example, bongo nets were found to more effectively catch small larvae but not large larvae relative to ring nets in an arctic fjord off Greenland (Swalethorp et al. 2014) and relative to Tucker trawls in eastern Canada (Pepin and Shears 1997). Similarly, a comparison of four types of sampling gear found significant differences in larval walleye pollock, *Theragra chalcogramma*, catch in the Gulf of Alaska (Shima and Bailey 1994). Habtes et al. (2014) also demonstrated that three net types strongly affected larval fish catch in the Gulf of Mexico. These studies and ours exhibit the need to evaluate and correct for differences in sampling efficiency when comparing larval fish abundances.

In addition to transitioning from ring to bongo nets in 1978, another major methodological change to CalCOFI sampling occurred in 1969. In this year the depth of net tows was changed from 140 to 210 m and silk nets with 0.55 mm mesh were replaced with nylon, 0.505 mm mesh nets. To evaluate the effects of these changes 42 tows were conducted in summer 1968 at station 93.3 30.0 (10 miles west of La Jolla, CA) (Smith 1974). Analysis of those data showed that zooplankton density was 1.37 times higher in the 210 m than 140 m tows. Interestingly, the zooplankton density was also 1.37 times greater in bongo versus ring net, thus making comparisons of zooplankton collected between 1951 and 1969 directly comparable to samples from 1979 to the present without correcting for sampling effects (Ohman and Smith 1995). At present, larval fish data from these samples is not available, and it is unknown if sampling biases for larval fishes cancel out between the earliest and current periods. Enumeration of larval abundances from the 1968 samples should be conducted to evaluate potential effects of transitioning from 140 to 210 m sampling depths and from silk to nylon mesh.

Our results demonstrated that there is systematic bias to estimates of larval fish abundance associated with the transition from ring to bongo nets in 1978. To ensure accuracy of larval fish time series analyses, corrections should be applied to *Cyclothone* spp., *Dio-genichthys* spp., *Engraulis mordax*, and *Vinciguerria* spp. Further, additional paired samples should be collected to improve sample sizes for other commercially and ecologically important species such as Pacific sardine (*Sardinops sagax*) and blue lanternfish (*Tarletonbeania crenularis*) that were mostly absent 1977–78 but have become more common at present. In addition, 1968 samples that evaluated the effect of changing net types, mesh size and tow depth should be sorted and analyzed to elucidate further potential effects on larval fish abundance estimation. Finally, studies on ichthyoplankton dynamics that utilized data pre and post implementation of bongo nets should be reanalyzed to ensure that the conclusions are robust to the net effects.

ACKNOWLEDGEMENTS

We greatly appreciate the effort of staff who collected the samples and those who sorted and identified the larvae in the laboratory. We thank Marc Fischer from Hydro-Bios for allowing us to use the illustrations in Figure 1. Discussion with Rasmus Swalethorp helped improve the manuscript. We thank two anonymous reviewers for helpful comments that improved this manuscript.

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