



Mesopelagic fish assemblages across oceanic fronts: A comparison of three frontal systems in the southern California Current Ecosystem

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ABSTRACT

With strong horizontal gradients in physical properties, oceanic frontal regions can lead to disproportionately high biological productivity. We examined cross-frontal changes in mesopelagic fish assemblages at three separate frontal systems in the southern California Current Ecosystem (CCE) as part of the CCE Long Term Ecological Research program: the A-Front sampled in October 2008, the C-Front in June/July 2011, and the E-Front in July/August 2012. We analyzed the differential effects of front-associated regions on density and species composition of adult migratory and non-migratory fishes and larvae, and the larval to adult ratio (as a possible index of a population growth potential) for migratory and non-migratory species. The fronts did not have a strong effect on densities of any subset of the mesopelagic fish assemblage. The species composition of the vertical migratory fishes (and their larvae) was typically altered across fronts, with different assemblages present on either side of each front. The migratory assemblages at the fronts themselves were indistinguishable from those at the more productive side of the frontal system. In contrast, the assemblage composition of the non-migratory fishes was indistinguishable between regions across all three of the fronts. The differences between the Northern and Southern assemblages at the A-Front were primarily based on biogeographic provinces, while the assemblages at the E-Front were largely distinguishable by their oceanic or coastal-upwelling zone associations. These results generally confirm those of previous studies on frontal systems in the California Current Ecosystem and elsewhere. The ratio of larvae to adults, a potential index of population growth potential, was altered across two of the fronts for migratory species, elevated on the colder side of the A-Front and the warmer side of the E-Front. This finding suggests that fronts may be regions of enhanced reproduction. The larvae to adult ratio was indistinguishable for non-migratory species at all three frontal systems. The non-migratory component of the community was little influenced by the presence of a front, apparently because the regions of strongest horizontal spatial gradients were too shallow to be experienced directly. We speculate that there was no change in larval community composition and population growth index at the most dynamic frontal system (C-Front) compared to the other fronts surveyed because the frontal feature was short-lived relative to the time scale for population growth of the fish. However, the difference in results of the C-Front may also be due to a change in methodology used in this study. If mesoscale features such as fronts increase in frequency off the California coast in the future as predicted, they have the potential to alter population growth potential and restructure mesopelagic fish assemblages, which are dominated by migratory species.

1. Introduction

The California Current Ecosystem (CCE) is a dynamic system with complex mesoscale features, including fronts, eddies, meanders, and jets, which are particularly common in the core California Current region off central and southern California (Checkley and Barth, 2009; Powell and Ohman, 2015). Fronts occur where two distinct water masses meet, and are characterized by strong horizontal gradients in physical properties such as temperature, salinity, and density. Fronts

vary in size, strength, duration, and mechanism of formation (Sournia, 1994). Fronts are typically associated with enhanced along-front currents (Sournia, 1994; de Verneil and Franks, 2015), and the physical dynamics at a front may lead to aggregations or accumulation of organisms (Franks, 1992). Frontal regions are often accompanied by elevated primary production (Chekalyuk et al., 2012; Taylor et al., 2012), zooplankton density (Powell and Ohman, 2015; Ohman et al., 2012), and density of higher trophic levels (Hoefer, 2000; Polovina et al., 2001; Doniol-Valcroze et al., 2007).

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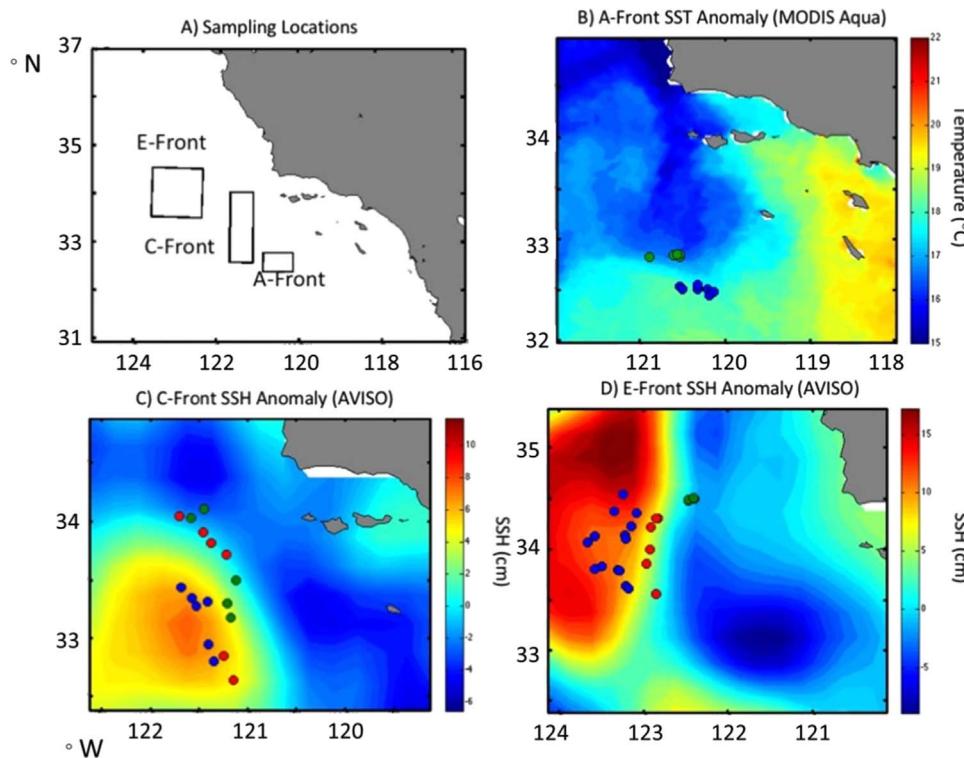


Fig. 1. A) Locations of each of the 3 frontal systems in the Southern California Current System. MOHT trawl sampling locations at the: B) A-front (overlaid on satellite-derived sea surface temperature (SST)), sampled from 20 to 27 October 2008, C) C-front (overlaid on satellite-derived sea surface height (SSH)), sampled from 18 June–17 July 2011, and D) E-front (SSH), sampled from 30 July–25 August 2012. Southern and Offshore stations are indicated by blue points, frontal stations by red, and Northern and Coastal stations by green.

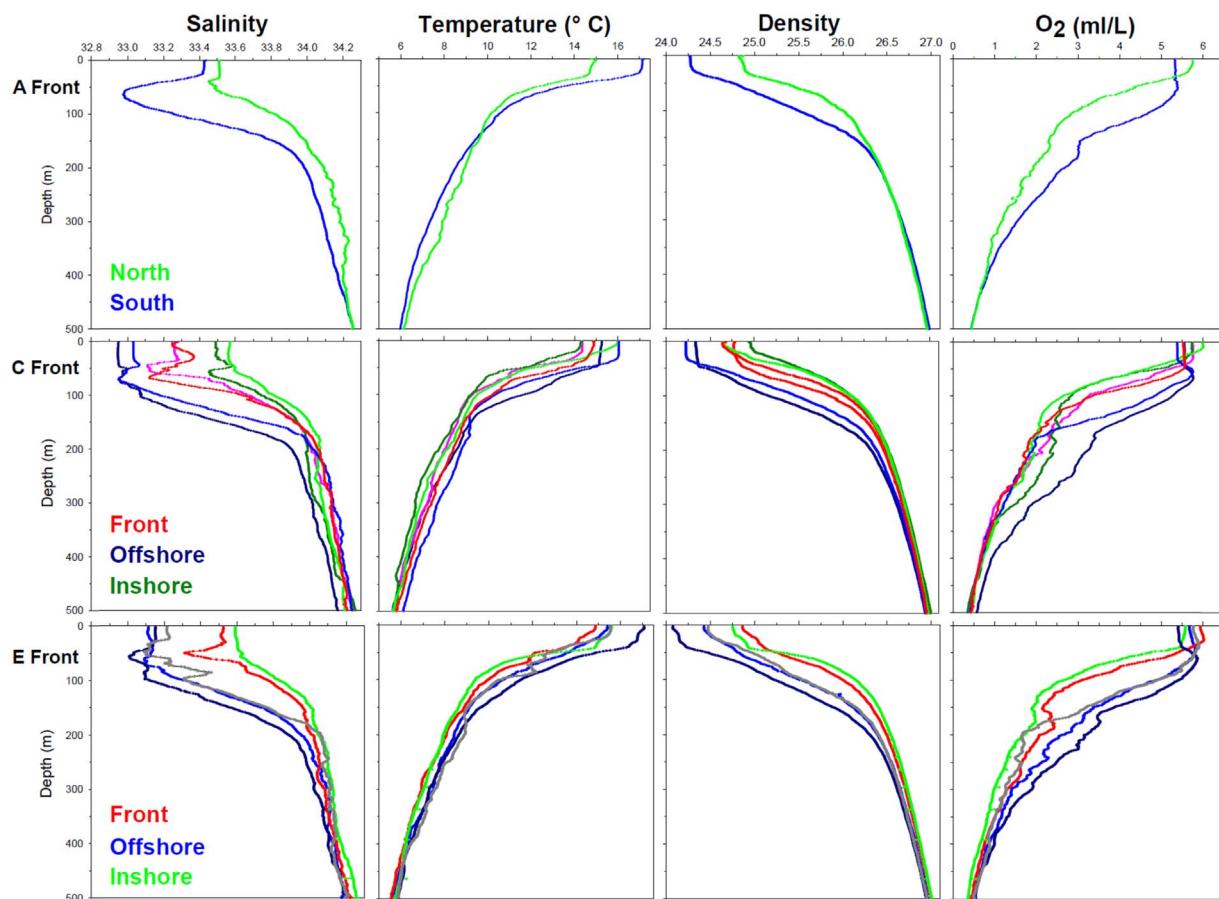


Fig. 2. Salinity, temperature, density, and oxygen profiles for each of the A, C, and E-Fronts. Each individual trace is the mean for a single sampling Cycle, with the northern (A-front) and coastal (C-front and E-front) stations represented in shades of green, frontal stations in red and pink, and southern (A-front) or offshore stations (C-front and E-front) in shades of blue and grey.

A recent study found that the frequency of satellite-detectable fronts in the CCE is increasing (Kahru et al., 2012). As there can be disproportionately high biological production at frontal features, an increase in frontal frequency could enhance integrated total productivity of the CCE region, with implications for fisheries, carbon transport to the deep sea, and marine spatial management. The horizontal gradients at oceanic fronts typically diminish with depth, but may extend as deep as 1000 m (Bower et al., 1985). The frontal gradients in the present study are slight or undetectable by 200 m depth (Figs. 1, 2, and S1), below which lies the deep scattering layer (DSL), an acoustically-detected midwater aggregation of mesopelagic organisms that is ubiquitous throughout the ocean (Currie et al., 1969; Tont, 1975; Irigoien et al., 2014). The mesopelagic fauna that comprises the DSL is an often overlooked component of oceanic ecosystems. However in the CCE, mesopelagic fish biomass is equal to or exceeds the biomass of the well-studied epipelagic clupeoid fishes (e.g., sardines, anchovies; Davison et al., 2015). Mesopelagic fishes are important forage for a number of predators such as tunas and billfishes (Bertrand et al., 2002; Potier et al., 2007), squids (Field et al., 2007), marine mammals (Pauly et al., 1998), and seabirds (Thompson et al., 1998). Mesopelagic fish are known to respond to environmental variability in physical and chemical factors, such as dissolved oxygen (Koslow et al., 2011, 2013; Netburn and Koslow, 2015). Here, we consider the responses of the mesopelagic fish community to the mesoscale horizontal gradients in temperature, salinity, and oxygen concentration expressed at fronts.

The CCE is a transitional region of the Pacific, with Subarctic waters transported southward into the region via the California Current, Subtropical waters transported northward from the Baja region, and Central Pacific Gyre waters at its western edge (Bograd and Lynn, 2003; Checkley and Barth, 2009). The dominant species collected at a site can be indicators of prevailing oceanographic and climate patterns (Moser and Smith, 1993; Beamish et al., 1999; Hsieh et al., 2009; Koslow et al., 2011). Mesopelagic fish species in the CCE generally fall into one of two assemblages based on their biogeographic affinities: Subarctic-Transition Zone and Subtropical-associated (including North Pacific Subtropical gyre) assemblages. There is additionally a distinction between species typically found in high abundance in the coastal upwelling zone and those that are generally more abundant in offshore oceanic regions causing a nearshore-offshore distinction between assemblages.

All adult mesopelagic fish have daytime minimum depths below 200 m depth, with a portion of the assemblage that migrates vertically into surface waters at night (Frost and McCrone, 1979; Watanabe et al., 1999) where the fishes are potentially influenced by frontal gradients. Mesopelagic fish assemblages are commonly separated into two primary categories based on the diel vertical migration propensity of the adults: Non-migrators whose adults remain in mesopelagic depths (> 200 m) both day and night and Migrators that traverse between the mesopelagic and epipelagic zones on a daily basis. Larval forms of all mesopelagic fishes live primarily in the epipelagic zone (Moser, 1996; Bowlin, 2015). The different ways in which these three groups—Non-migrators, Migrators, and Larvae—are distributed in the water column suggest they experience different environmental conditions and environmental gradients. In the case of epipelagic-intensified frontal features, the distinctive distributions of these groups provide an opportunity to test the differential influence of fronts on the density, assemblage composition, and population growth potential of different segments of the mesopelagic fish assemblage.

Three different deep-water frontal systems were studied in the southern sector of the California Current System Long-Term Ecological Research (CCE-LTER) region between 2008 and 2012 (Fig. 1 and S1). The A-Front was oriented on an East-West axis, where colder saltier waters from the north met warmer fresher southern waters (Landry et al., 2012), and was a relatively stationary and persistent feature of the CCE (Haury et al., 1993; Chereskin and Niler, 1994; Lara-Lopez et al., 2012). However, more transient and dynamic fronts are common in the CCE, arising at the edge of mesoscale features such as eddies, jets,

and filaments (Checkley and Barth, 2009), such as the California Current Front (C-Front, Brzezinski et al., 2015; Krause et al., 2015) surveyed in 2011 and the Eddy-Front (E-Front) studied in 2012 (Bednaršek and Ohman, 2015; de Verneil and Franks, 2015). These features differed both from each other and from the A-Front in characteristics, intensity, and persistence, thus providing opportunities to analyze how different types of fronts affect mesopelagic fish density, species composition, and population growth potential.

In this paper we seek specifically to answer the following questions:

- 1) Is the density of mesopelagic fishes enhanced at fronts?
- 2) Is the species composition of mesopelagic fish assemblages altered across frontal regions?
- 3) Is population growth potential (using larval to adult ratio as a proxy) enhanced at the front or either side of the front?
- 4) Are the effects of fronts different for vertically migrating fishes than for non-migrating fishes?
- 5) Are effects of fronts similar across different frontal systems?

2. Methods

2.1. Sampling locations

All cruises took place on the R/V *Melville*, and utilized the same quasi-Lagrangian sampling design (Table 1). Each cruise consisted of a series of experimental Cycles, in which a satellite-tracked drifter was followed for 3–4 days, with comprehensive physical and biological sampling conducted in close proximity to the drifter (Landry et al., 2009, 2012; Ohman et al., 2012). Fronts were identified prior to sampling using satellite imagery of temperature, ocean color, and sea surface height (SSH) (Fig. 1, S2–S4). More detailed site surveys with both a SeaSoar and Moving Vessel Profiler (Ohman et al., 2012, 2013) were used to identify specific locations for the drifter deployments. A series of closely-spaced CTD casts were conducted across each front. These data are presented in Fig. S1. These casts did not always capture the subsurface component of the front. Multiple CTD casts were conducted throughout each 3–4 day Cycle to measure temperature, salinity, oxygen, and fluorescence, and collect water for other experiments. We report on the means for each experimental Cycle in Fig. 2 to demonstrate the contrast in the salinity, temperature, and oxygen concentration present in the vicinity of the fish sampling locations.

The A-Front study was located south of Point Conception and offshore of the Channel Islands, from ~32.25–32.75°N and ~120–121°W, and sampling occurred from 20 to 27 October 2008 (Fig. 1a & b). The A-Front was characterized by strong gradients in both temperature and chlorophyll concentration (Landry et al., 2012). Responses of the density, biomass, and community composition of the mesopelagic fish assemblage in relation to the front were reported in Lara-Lopez et al. (2012), and many of the results are included in this study for comparison. Assignment of species-specific migratory behavior (Table S1) has, however, been revised based on Davison et al. (2015) and Froese and Pauly (2015). There was no direct sampling of mesopelagic fishes at the A-Front itself, and we report on the two adjacent regions, the denser, colder, and saltier Northern region and the less dense, warmer, and fresher Southern region (Fig. 1a & b, 2a).

Table 1
Frontal systems sampled in this study.

System	Dates	Characteristics
A-Front	20–27 October 2008	boundary between N/S waters, stable, long-lasting
C-Front	18 June–17 July 2011	eddy-associated, frontogenesis
E-Front	28 July–26 August 2012	eddy-associated, stable

The California Current Front (C-Front) study took place at $\sim 32.5\text{--}34^{\circ}\text{N}$ and $\sim 121\text{--}122^{\circ}\text{W}$, from 18 June–17 July 2011 (Fig. 1a & c, 2b). The C-Front was located at the confluence of two eddies and was highly dynamic in space and time. The front shifted during the sampling period, which may have captured a period of frontogenesis (Brzezinski et al., 2015; Krause et al., 2015). The “Offshore” stations were located within a warm-core eddy, “Inshore” stations toward a cold-core eddy, and “Frontal” stations were located where the water masses met.

The Eddy Front (E-Front) study was located at $\sim 33.5\text{--}34.5^{\circ}\text{N}$ and $\sim 122.75\text{--}123.75^{\circ}\text{W}$, and was sampled from 28 July–26 August 2012 (Fig. 1a & d). The E-Front was more stable over the sampling period than the C-Front, but was similarly characterized by a paired offshore warm-core eddy and nearshore cold-core eddy (Bednaršek and Ohman, 2015). Based on differences in salinity and density, we designated stations as Inshore, Offshore, or Frontal (Fig. 2c).

We sampled mesopelagic fishes at each region (Northern/Southern for A-Front, Inshore/Offshore/Frontal for C and E-Fronts) with multiple oblique tows of a Matsuda-Oozeki Hu Trawl net (MOHT, Oozeki et al., 2004) with a 5 m^2 mouth opening and a net mesh size of 1.6 mm. For the A-Front and E-Front surveys, we typically collected daytime samples to ~ 500 m and nighttime samples to 150–200 m. We calculated the volume of water filtered by multiplying the distance travelled measured using a calibrated TSK flowmeter by the area of the trawl mouth opening. Maximum depth was measured by using a temperature depth recorder mounted to the frame of the MOHT net. For the C-Front study, we modified the MOHT frame with an opening-closing cod end system with a 1.7 mm mesh net. Net opening was typically triggered on ascent from 1000 m. There was contamination within the depth-stratified samples of the C-Front study, so we integrated them over the full depth sampled (0–1000 m) and estimated volume sampled based on the proportion of time the net was actually fishing.

We separated all fish at sea from the invertebrate component of the catch, and preserved them in 10% formaldehyde buffered with sodium tetraborate. We identified all fish and larvae to the lowest possible taxonomic level, which was typically species, and assigned diel vertical migration behavior as per Davison et al. (2015; Table S1). Each fish was assigned as either a diel vertically-migrating adult or juvenile (“Migrator”), non-vertically migrating adult or juvenile (“Non-migrator”), or “Larvae.” For analyses of the Non-migrators, only deep trawls were considered. Larvae were classified as such based on ontogenetic characteristics (Moser, 1996). Given the mesh size of the trawl, we typically captured only the larger size class of larvae. Biogeographic provinces of abundant species were assigned based on published literature (Moser et al., 1987; Moser and Smith, 1993; Brodeur and Yamamura, 2005; Hsieh et al., 2005, 2009). We did not include incidentally-collected epipelagic and demersal taxa in any of the analyses.

3. Density

Because of the large size range between different species including in the study, count data were used for the analyses as large rare organisms could dominate biomass. Count data for each species were standardized by dividing the count by the volume filtered and integrating over depth (indivs. m^{-2}) to obtain densities for each fish species sampled. We tested for differences in densities between regions for each group of Migrators, Non-migrators, and Larvae using the nonparametric Mann-Whitney *U* test (to test between the two populations, North and South) for the A-Front and the Kruskal-Wallis analysis of variance (to test between $>$ two populations, Inshore, Offshore, and Frontal) for the C- and E-Fronts.

4. Species composition

The standardized counts were then $\log(x + 1)$ transformed to reduce skew and expressed as % total density by species for each trawl

before calculating Bray-Curtis distances. Data were expressed as % total to address the differences in sampling design. At the C-Front, where sampling occurred to 1000 m, there were generally lower abundances at the deeper depth, which means that fewer fish were captured over an equivalent volume. Using Primer software, we used non-metric multidimensional scaling (nMDS) to visualize the differences in community composition among stations and Analysis of Similarity (ANOSIM) to test whether different regions had significantly different assemblages. Similarity Percentage (SIMPER) analysis was used to determine the relative contribution of specific taxa to the differences in assemblages. Analyses were conducted separately on Migrators, Non-migrators, and Larvae first for all three frontal systems combined with groups assigned by frontal system (ie., A,C,E), and for each individual front with assignments based on frontal region.

5. Larval to adult ratio

Unfortunately, we do not have sufficient life history data on most species to be able to estimate the age of most larvae in this study (N. Bowlin, pers. comm.). However, larvae of many species considered in this study likely metamorphize between 30 and 70 days (Moku et al., 2001, Gartner et al., 1991, Smoker and Pearcy, 1970), a period during which the fronts could have persisted (S2-S4). To test whether the presence of the front affected population growth potential, we calculated the ratio of larvae to adults for each species at each sampling station. This index can be elevated due to either increased egg production or decreased larval mortality. We calculated the mean of these ratios separately for all Migrators and Non-migrators at each region of each front. We also independently calculated the larval to adult ratios for the 20 individual species for which our gear collected sufficient numbers of both adults and larvae, reported in Fig. S5. The non-parametric Mann-Whitney *U* test (for two populations at the A-Front) and Kruskal-Wallis test (for the three populations at each of the C- and E-Fronts) were used to test for differences among these ratios between regions at each frontal system, followed by pairwise comparisons using the Dwass-Steel-Critchlow-Fligner method (Hollander and Wolfe, 1999).

6. Results

All trawl locations, times, depths, and volume filtered are reported in Table 2.

6.1. Density

A list of all species collected over the course of the 3 studies is included in Table S1. There were no significant differences across fronts in the total densities of either Migrators or Non-migrators, apart from Migrators across the C-Front ($P = 0.05$, Table 3). There was a significant difference in Larval density ($p < 0.03$) between the Northern and Southern regions of the A-Front, with higher density in the south, and no significant differences in Larval densities at either the C- or E-Fronts.

6.2. Community composition

6.2.1. Comparisons between A, C, & E-Front assemblages

The three frontal studies had heterogeneous compositions of Migrators ($p < 0.001$) and Larvae ($p < 0.001$), which was reflected in significant pairwise differences between each pair of studies (Table 4). However, the stress values > 0.20 should be noted for the nMDS of both Migratory and Larval assemblages, indicating the two-dimensional scaling is not the best representation of the assemblage differences. Although there was weak heterogeneity among Non-migrators (ANOSIM, $p < 0.05$, R -statistic = 0.152), a posteriori pairwise comparisons revealed that there was no significant difference between the Non-

Table 2

Date, location, time, duration, depth, and volume of water filtered for all trawl stations in this study. Duration was not available for the A-Front study. Volume of water filtered was estimated based on deployment time for station 2-1, when there was an error with the flowmeter.

Station A-Front	Date	Start Lat	Start Lon	Start Time	Duration (min)	Depth (m)	Vol. Filtered (m ³)
5-1	10/22/2008	32° 49.44'	120° 53.04'	06:52	–	741	39062.0
5-3	10/23/2008	32° 50.52'	120° 36.30'	14:35	–	986	31451.0
5-4	10/23/2008	32° 51.66'	120° 31.92'	20:24	–	841	34676.0
5-5	10/24/2008	32° 51.24'	120° 31.86'	00:51	–	213	16192.0
5-6	10/24/2008	32° 51.24'	120° 34.08'	04:30	–	191	15331.0
6-1	10/26/2008	32° 32'.34'	120° 31.62'	05:12	–	171	18156.0
6-2	10/26/2008	32° 30.72'	120° 30.30'	06:50	–	719	39831.0
6-4	10/26/2008	32° 30.60'	120° 19.38'	20:42	–	784	37694.0
6-5	10/27/2008	32° 33.18'	120° 19.14'	00:02	–	207	16642.0
6-6	10/27/2008	32° 30.30'	120° 12.18'	08:44	–	754	38049.0
6-7	10/27/2008	32° 27.66'	120° 10.62'	14:29	–	691	43245.0
6-8	10/27/2008	32° 26.82'	120° 11.28'	17:31	–	672	44445.0
6-9	10/27/2008	32° 28.86'	120° 8.16'	22:55	–	192	17626.0
C-Front							
1-1	6/23/2011	34° 2.74'	121° 42.24'	20:28	187	900	57863.2
1-2	6/24/2011	33° 54.85'	121° 27.66'	21:40	124	1000	38699.8
1-4	6/25/2011	33° 43.32'	121° 13.09'	21:10	126	1000	31361.4
1-5	6/26/2011	33° 49.45'	121° 22.70'	10:28	158	1000	46432.7
2-1	6/27/2011	33° 26.35'	121° 40.91'	14:00	158	1000	NA
2-2	6/28/2011	33° 20.97'	121° 34.35'	14:44	158	1000	45475.5
2-3	6/28/2011	33° 16.53'	121° 31.93'	23:51	143	1000	44513.3
3-1	6/29/2011	34° 2.00'	121° 35.02'	21:46	85	550	35525.9
3-3	7/1/2011	34° 6.41'	121° 26.95'	14:05	152	1000	63976.0
4-1	7/7/2011	33° 30.24'	121° 6.95'	14:30	107	1054	66065.1
4-2	7/8/2011	33° 18.31	121° 12.35'	14:26	161	1133	49366.7
4-3	7/9/2011	33° 10.52'	121° 10.60'	00:05	125	1164	51858.1
5-1	7/10/2011	33° 18.84'	121° 24.89'	14:25	138	1016	42499.8
5-2	7/11/2011	32° 57.02'	121° 23.91'	14:20	222	1299	50512.8
5-3	7/12/2011	32° 47.94'	121° 20.60'	23:57	123	1136	41679.6
6-1	7/14/2011	32° 51.02'	121° 14.87'	14:09	146	1387	32145.5
6-2	7/15/2011	32° 38.52'	121° 8.58'	23:58	142	1000	33030.7
E-Front							
0-1	7/28/2012	33° 7.59'	– 118° 22.11'	18:20	81	550.8	33263.7
1-1	8/6/2012	34° 18.24'	– 122° 49.44'	16:07	123	949.3	38053.0
1-2	8/6/2012	34° 18.12'	– 122° 50.76'	18:57	28	60	11786.9
1-3	8/7/2012	34° 12.96'	– 122° 54.54'	03:24	65	178.2	30743.7
1-4	8/7/2012	34° 0.12'	– 122° 55.68'	13:18	130	942.2	39322.6
1-5	8/7/2012	33° 51.48'	– 122° 57.96'	23:07	124	873.6	37324.3
1-6	8/9/2012	33° 33.72'	– 122° 51.18'	01:06	65	191.5	26006.5
2-1	8/10/2012	34° 21.60'	– 123° 5.16'	12:20	125	1053.3	34592.2
2-2	8/10/2012	34° 13.74'	– 123° 9.00'	18:28	144	1065.6	41625.4
2-3	8/11/2012	34° 8.10'	– 123° 13.02'	00:23	65	287.4	25436.4
2-4	8/11/2012	33° 47.94'	– 123° 18.00'	12:47	148	1039.6	41811.7
2-5	8/11/2012	33° 47.10'	– 123° 17.16'	16:37	132	1127.5	39530.6
2-6	8/11/2012	33° 38.34'	– 123° 12.48'	22:36	66	269.9	19094.0
2-7	8/12/2012	33° 36.60'	– 123° 10.50'	00:36	64	210.4	24645.0
3-1	8/13/2012	34° 28.74'	– 122° 27.90'	15:17	107	510.6	39004.8
3-2	8/14/2012	34° 28.98'	– 122° 28.32'	03:08	64	101.6	28939.3
3-3	8/14/2012	34° 29.76'	– 122° 23.46'	14:57	266	868.4	95303.5
3-4	8/15/2012	34° 30.48'	– 122° 24.00'	02:10	67	152.7	29575.5
4-1	8/15/2012	34° 32.58'	– 123° 14.70'	21:33	67	185.8	28420.3
4-2	8/16/2012	34° 22.32'	– 123° 20.58'	14:52	136	854.3	45933.1
4-3	8/17/2012	34° 7.92'	– 123° 34.38'	15:08	126	861.4	51358.2
4-4	8/18/2012	34° 4.14'	– 123° 39.66'	01:09	68	165.1	26022.9
5-1	8/18/2012	34° 6.42'	– 123° 12.54'	21:06	61	168.8	37755.8
5-2	8/19/2012	33° 50.04'	– 123° 29.34'	12:41	272	2836.5	64807.2
5-3	8/19/2012	33° 48.42'	– 123° 34.92'	22:23	68	153.2	31971.0

migratory assemblages of the C- and E-Fronts ($p = 0.86$, $R = -0.072$). The Non-migratory C- and E-Front assemblages are therefore combined in the nMDS analysis (Fig. 3b), while we maintained the distinctions between the three studies for the Migratory fishes and Larvae (Fig. 3a & c). We used SIMPER analysis to obtain relative differences in species' density between groups (Fig. 3d-f), however SIMPER does not test for statistically significant differences between individual species' densities between groups. The Non-migratory assemblage of the A-Front study was differentiated through SIMPER analysis from the two more northern, eddy-associated fronts by relatively higher densities of *Cyclothona signata* and *Argyropelecus hemigymnus*, and lower *Cyclothona*

pseudopallida and *Argyropelecus sladoni* (Fig. 3e). These species all have relatively broad distributions in the North Pacific (Beamish et al., 1999), and the patterns of distribution we saw are not explained by distinctive biogeographic provinces (Beamish et al., 1999; Brodeur and Yamamura, 2005).

The Migratory assemblage of the A-Front study had higher relative densities of the subtropical species *Triphoturus mexicanus* and *Vinciguerria nimbaria* and lacked the Subarctic-Transition Zone *Stenobrachius leucopsarus* and *Diaphus theta* that were abundant in the more northerly fronts (Fig. 3d). The A-Front study larval community consisted of relatively high densities of Subarctic-Transition Zone

Table 3

Median densities of vertical migrants, non-vertical migrants, and larvae of mesopelagic fishes at each region sampled for each of the three fronts. The reported p-values are based on non-parametric tests for difference in medians (Mann-Whitney *U* test for the A-Front, and Kruskal-Wallis one-way analysis of variance for both the C- and E-Fronts).

A-Front (P0810)	Indivs m ⁻² (25–75 th percentiles)		p-value
	South n = 8	North n = 5	
Migrants	1.96 (1.79–4.43)	3.65 (2.03–7.79)	0.31
Non-migrants	7.37 (0.60–8.53)	4.76 (0.84–5.70)	0.31
Larvae of mesopelagic fishes	0.73 (0.63–2.41)	0.19 (0.14–0.48)	0.03*
Offshore			
Front		Inshore	
C-Front (P1106)	n = 6	n = 6	n = 5
Migrants	0.92 (0.40–1.07)	0.76 (0.44–0.91)	2.28 (1.17–4.53)
Non-migrants	3.99 (3.75–5.38)	4.68 (3.14–8.62)	3.57 (3.02–4.33)
Larvae of mesopelagic fishes	0.29 (0.21–0.59)	0.36 (0.16–0.44)	0.19 (0.12–0.25)
E-Front (P1208)	n = 5	n = 14	n = 4
Migrants	2.07 (0.96–5.18)	1.84 (1.41–9.81)	5.79 (2.54–7.96)
Non-migrants	1.40 (0.89–2.27)	2.77 (0.81–3.62)	2.04 (0.54–5.01)
Larvae of mesopelagic fishes	0.26 (0.08–1.33)	0.22 (0.11–0.55)	0.13 (0.07–0.22)

Bathylagoides wesethi, *Protomyctophum crockeri*, and *Chauliodus macouni*, and low *Lipologus ochotensis* compared with the C- and E-Fronts. The subtropical *V. nimbaria* larvae were only present at the A-Front, while Subtropical-Transition Zone *T. mexicanus* larval densities were substantially higher there as well. Several larval species were entirely absent at the A-Front, including the Subarctic-Transition Zone *Nannobrachium regale*, *Tactostoma macropus*, and *Leuroglossus stibius*, as well as the subtropical/transitional *Ceratoscopelus townsendi*.

6.2.2. Non-migrants

In comparisons of Non-migrants across individual fronts, we detected significant spatial heterogeneity in the assemblages by region at only the E-Front (Fig. 4a–c, Table 3; p < 0.05; A-Front: p = 0.14, C-Front: p = 0.09). However, none of the pairwise comparisons at the E-Front were found to be significantly different (Frontal/Offshore: p = 0.07, Frontal/Inshore: p = 0.10, Offshore/Inshore: p = 0.43).

6.2.3. Migrants

Comparing assemblages of Migrants across individual frontal systems (Fig. 5a–c, Table 3), there was significant heterogeneity of

assemblages across all three fronts (p < 0.05), though there were no pairwise differences between the Frontal and Inshore assemblages at either of the C- (p = 0.20) or E-Fronts (p = 0.29). The assemblage differences at the A-Front were caused by higher relative densities of the subtropical *V. nimbaria*, *Lamпадена urophoas*, and *C. townsendi* on the Southern side, and higher densities of Subarctic-Transition Zone *Idiacanthus antrostomus*, *D. theta* and *Tarletonbeania crenularis* on the Northern side (Fig. 5d). At the C-Front, we measured elevated densities of *D. theta*, and *Diogenichthys atlanticus* on the Offshore side, and elevated *L. ochotensis*, *T. mexicanus*, and *N. ritteri* at the Inshore and Frontal regions (Fig. 5e). The E-Front varied from this pattern, with elevated *C. townsendi*, *D. theta*, and *Nannobrachium ritteri* on the Offshore side, and high *L. stibius*, *T. mexicanus*, and *T. crenularis* at the Inshore and Front-associated regions (Fig. 5f). These patterns generally agree with coastal-oceanic distributions observed at larger scales (e.g., Davison, 2011).

6.2.4. Larvae

Larval assemblages were significantly different (p < 0.001) across the A-Front and E-Front (Fig. 6 a & c, Table 3), with the Frontal and Inshore assemblages of the E-Front indistinguishable from each other

Table 4

Results of Analysis of Similarity (ANOSIM) and a posteriori pairwise comparisons for species assemblages for all cruises combined and for each frontal system independently. For all studies combined, we conducted comparisons between frontal systems (A,C,E). For the individual frontal systems, we compared between frontal locations (pairwise comparisons columns). Subscripts for p-values are: A, C, or E demarcating each study, or F: Frontal, O: Offshore, I: Inshore. (See Figs. 3–6 for the nMDS ordination).

	p-value (R-statistic)	Pairwise Comparisons		
ALL CRUISES				
Grouped by study				
Migratory	***(0.537)	p_{A,I}	p_{A,E}	p_{I,E}
Non-migratory	*(0.152)	*(0.262)	* **(0.585)	0.86 (−0.072)
Larvae	***(0.267)	*** (0.440)	*** (0.270)	***
Grouped by frontal location		p_{F,O}	p_{F,I}	p_{O,I}
A-FRONT				
Migratory	*** (0.609)			
Non-migratory	0.143 (0.333)			
Larvae	*** (0.683)			
C-FRONT				
Migratory	* (0.178)	* (0.183)	0.20 (0.085)	* (0.31)
Non-migratory	0.09 (0.103)	–	–	–
Larvae	0.10 (0.121)	–	–	–
E-FRONT				
Migratory	*** (0.456)	* * (0.455)	0.29 (0.056)	* *
Non-migratory	* (0.364)	0.07 (0.405)	0.10 (0.667)	0.43 (0.127)
Larvae	*** (0.380)	* (0.364)	0.55 (−0.031)	* * (0.505)

*p < 0.05 *p < 0.01 **p < 0.001.

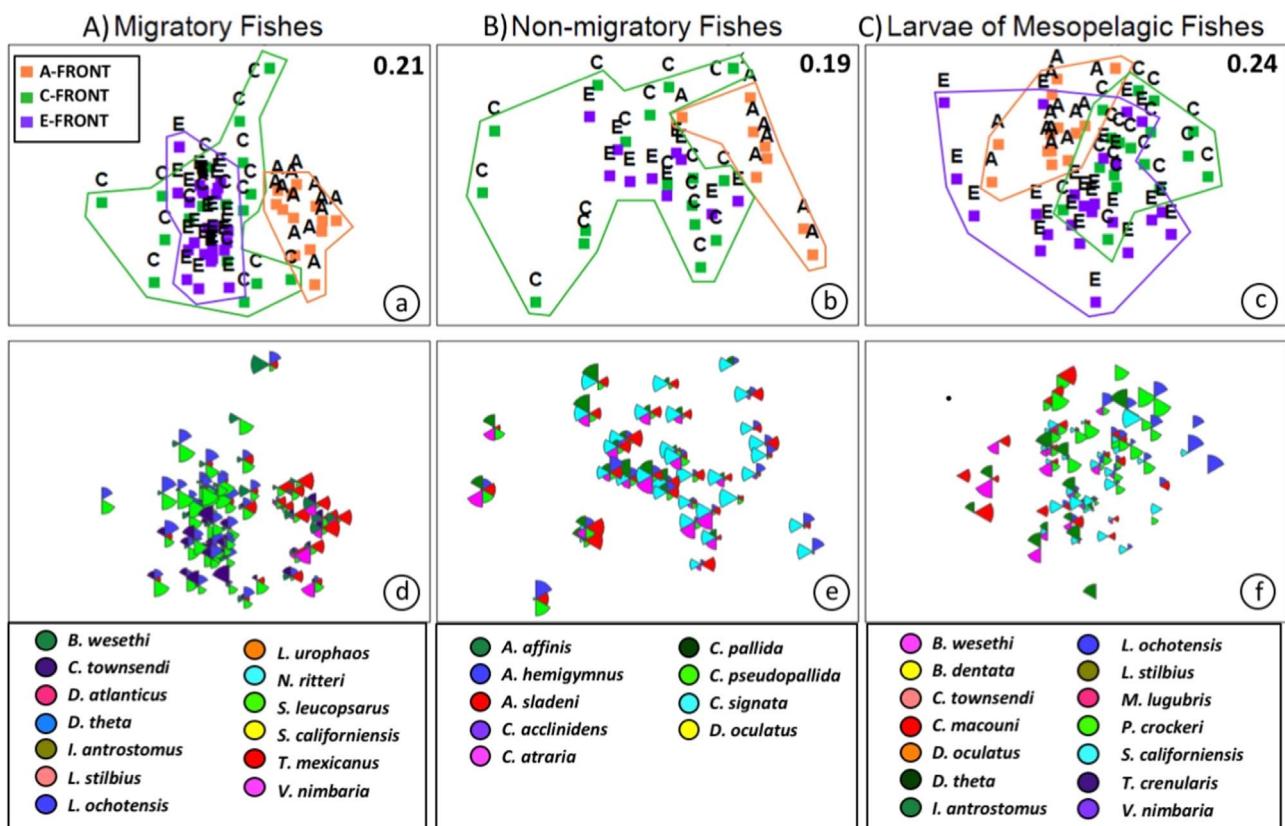


Fig. 3. nMDS plots of A) vertically migrating fishes, B) non-vertically migrating fishes, and C) larvae of mesopelagic species for all three fronts. The upper panel (a-c) for each nMDS analysis is color-coded by frontal system. The preassigned groups that are distinguishable from each other based on the ANOSIM test are outlined in solid lines. The lower panel of each nMDS analysis (d-f) shows a bubble plot indicating the relative densities of the species that were most informative for distinguishing between the systems according to the results of SIMPER analysis. We report the ANOSIM results and pairwise comparisons between regions in Table 3. The stress value, marked in the upper right-hand corner of each plot, is an indicator of how the distances on the nMDS plot represent the Bray-Curtis distances. Ordination with stress values of < 0.20 for two dimensions are considered to represent the true distances reasonably well.

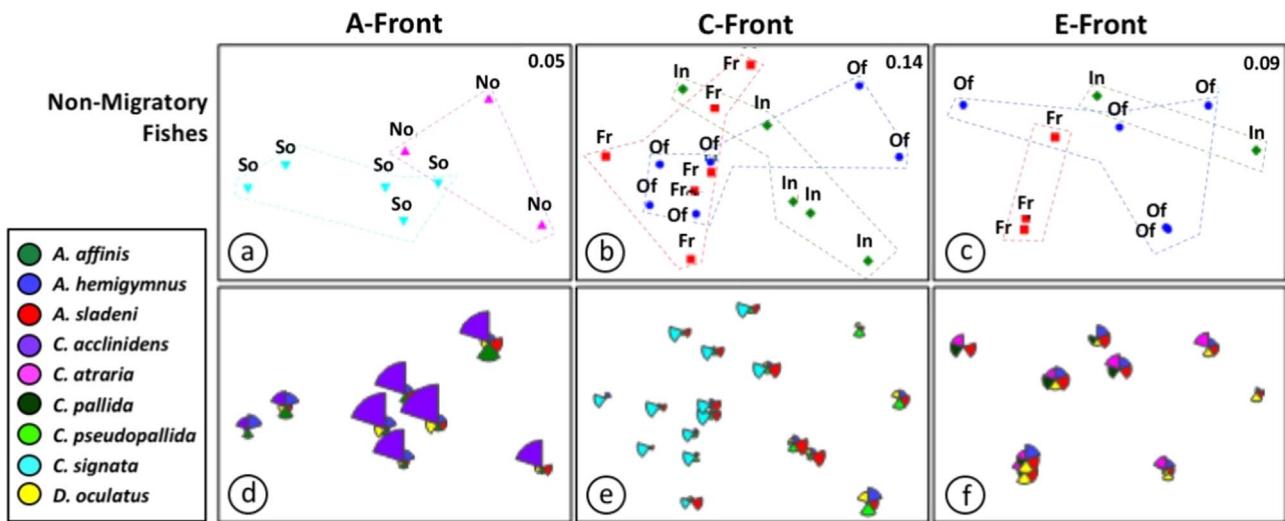


Fig. 4. nMDS plots of non-vertically migrating fishes. For each frontal system, the upper panel (a-c) of each nMDS analysis is color-coded by region. The regions are Offshore, Frontal, and Coastal for the C- and E-Fronts, and North and South for the A-Front. The preassigned groups that are distinguishable from each other based on the ANOSIM test are outlined in solid lines; faint dotted lines indicate regions that did not differ significantly. The lower panel (d-f) of each nMDS analysis shows a bubble plot indicating the relative densities of the species that were most informative for distinguishing between the regions according to the results of SIMPER analysis. We report the ANOSIM results and pairwise comparisons between regions in Table 3.

($p = 0.55$). The larval assemblages were not statistically distinguishable by region across the C-Front ($p = 0.10$, Fig. 6b). Larval assemblages at the Southern side of the A-Front were characterized by high densities of *V. nimbaria* and *D. theta* in the south (both completely absent in the north), and elevated densities of the broadly-distributed

Benthalbella dentata, and Subarctic-Transition Zone *C. macouni* and *T. crenularis* in the North (Fig. 6d). The Offshore side of the E-Front was characterized by high *I. antrostomus*, *S. californiensis*, *C. townsendi*, all warm-water associated species, while the Inshore and Frontal regions had high *C. macouni*, *T. macropus*, *T. crenularis*, and *L. stilbius* which are

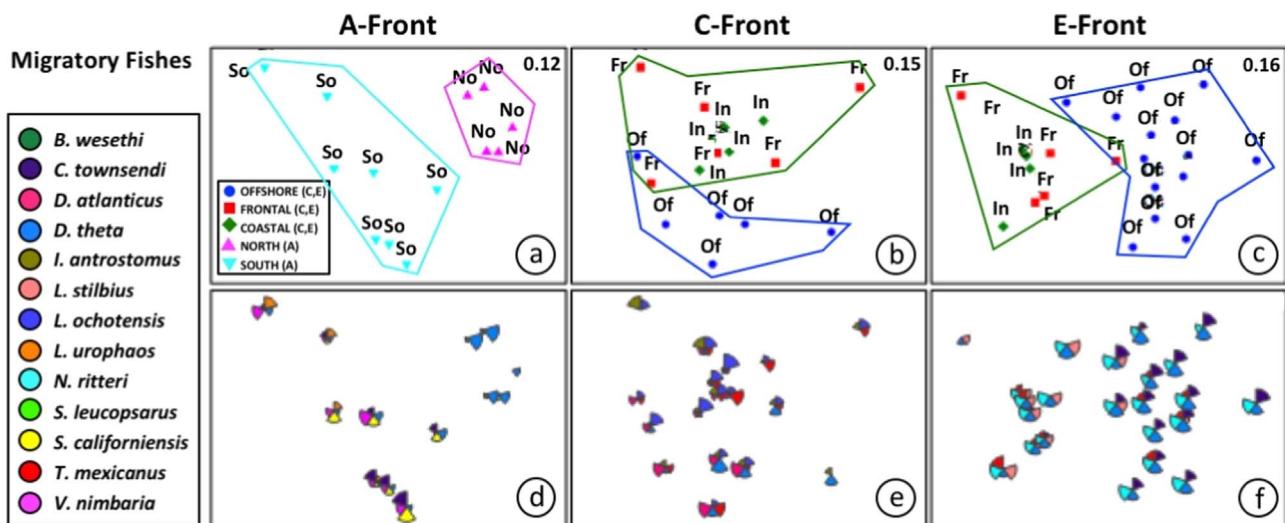


Fig. 5. nMDS plots of vertically migrating fishes. For each frontal system, the upper panel (a-c) of each nMDS analysis is color-coded by region. The regions are Offshore, Frontal, and Coastal for the C- and E-Fronts, and North and South for the A-Front. The preassigned groups that are distinguishable from each other based on the ANOSIM test are outlined in solid lines; faint dotted lines indicate regions that did not differ significantly. The lower panel (d-f) of each nMDS analysis shows a bubble plot indicating the relative densities of the species that were most informative for distinguishing between the regions according to the results of SIMPER analysis. We report the ANOSIM results and pairwise comparisons between regions in Table 3.

cold-water associated (Fig. 6f). There were a few species that were abundant at one region while entirely absent from others.

7. Larva to adult ratio

Due to the high number of zeroes (adults collected, but no larvae) in our data, we present the mean and individual ratios for each region of each front in Fig. 7, although we report p-values based on rank differences (Mann-Whitney U and Kruskal-Wallis). There was no significant difference in the mean ratio of larvae to adults (larvae per 100 adults, $\log(X + 1)$ transformed) for Non-migratory species at any of the frontal systems. For Migrators, we detected a significantly higher ratio of larvae to adults on the Northern side of the A-Front than the Southern side ($p < 0.001$), and also detected differences at all regions of the E-Front with the highest larvae to adult ratio in the Offshore region, followed by the Frontal region, and then the Inshore region ($p < 0.01$ for all pairwise comparisons). There was no significant difference in the ratios of larvae to adults for the C-Front ($p = 0.14$). We

report the larval:adult ratio of 20 individual species in Fig. S5. There were no significant differences in the ratios between regions for any individual species ($p > 0.05$).

8. Discussion

We found no change in density of vertically migrating and non-vertically migrating fishes between frontal regions at any of the three fronts (for the frontal regions sampled), and elevated density of Larvae at only the northern side of the A-Front relative to the southern side of that system. We observed front-associated changes in species composition for Migrators and Larvae, although not for Non-Migrators. The larval:adult ratio was enhanced in association with two of the three fronts for Migrators, with no change across frontal regions for Non-Migrators. Effects were generally diminished at the C-Front, which could be attributed to either the more transient nature of this feature or to the different trawling methodology.

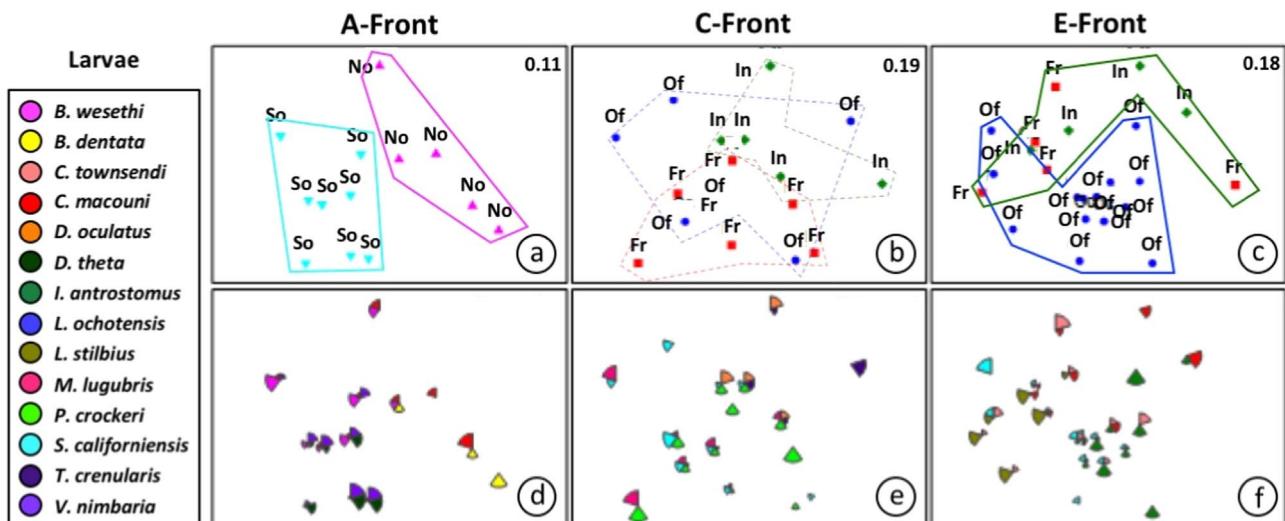


Fig. 6. nMDS plots of larvae of mesopelagic species. For each frontal system, the upper panel (a-c) of each nMDS analysis is color-coded by region. The regions are Offshore, Frontal, and Coastal for the C- and E-Fronts, and North and South for the A-Front. The preassigned groups that are distinguishable from each other based on the ANOSIM test are outlined in solid lines; faint dotted lines indicate regions that did not differ significantly. The lower panel (d-f) of each nMDS analysis shows a bubble plot indicating the relative densities of the species that were most informative for distinguishing between the regions according to the results of SIMPER analysis. We report the ANOSIM results and pairwise comparisons between regions in Table 3.

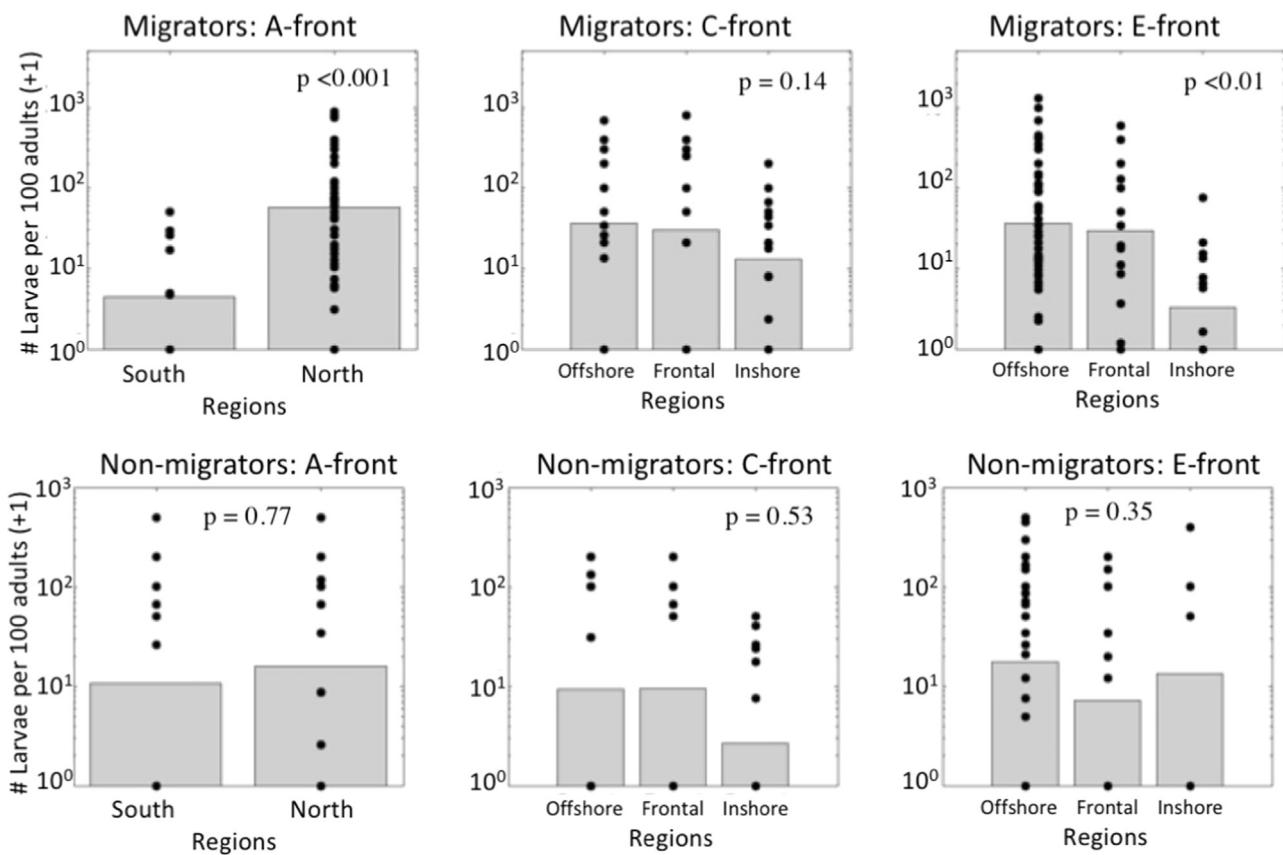


Fig. 7. Ratio of larvae per 100 adults (log(X + 1) transformed) for both vertically-migrating and non-migrating fishes. Bars indicate mean values of the ratios for all species, and points represent the ratio for each species at each station sampled in the region. See Fig. S1 for results for individual species.

8.1. Density

Due to the reassignment of migratory behavior for some species, our density results for the A-Front are slightly different from those of Lara-Lopez et al. (2012). In agreement with their analysis, we detected significantly elevated Larval density on the southern side of the A-Front, however we did not detect a significant difference in the densities of Migrators between the two sides of the front as they did. Still, densities of Migrators showed a tendency to be higher on the colder side of each of the three fronts, although significantly so only in the case of the C-Front Migrators. This result is in agreement with previous studies that have shown elevated densities of mesopelagic fishes at the cooler side of fronts within the southern CCE (Haury et al., 1993; Moser and Smith, 1993), as well as in the Atlantic Ocean (where most studies on the topic have occurred), with enhanced densities of mesopelagic fishes on the cooler side of an East-West oriented front (Backus et al., 1969), the edge of a warm-core ring (Olson and Backus, 1985), at the Angola-Benguela Frontal Zone (John, 2001), and at the Azores front (Angel, 1989), associated with colder and more productive waters. There is acoustic evidence that there is elevated fish densities at the frontal region of both the A-Front (Lara-Lopez et al., 2012) and the C-Front (Koslow, unpublished data). However, there was no sampling directly at the front in the A-Front study. At the C and E-Front, the trawl net may not have sufficiently sampled the frontal area, because we were limited by wind and current to towing across the front, integrating the community over as many as 10 nautical miles.

8.2. Assemblage composition

With little sunlight reaching mesopelagic depths, the resident fauna are ultimately dependent on primary productivity from the above

epipelagic zone to meet their energy demands. Zooplankton and fish transfer carbon into the deep sea through diel vertical migration and respiration (Steinberg et al., 2008a, b). The biomass of mesopelagic fish (Davison et al., 2013; Irigoien et al., 2014) and their prey (Steinberg et al., 2008a, b) correlates strongly with surface productivity at basin and global scales, and here we tested for effects across small-scale features. We did not detect a significant effect of the frontal gradients on the composition of Non-migrators across regions of any of the fronts that we studied, although there were some differences between the different frontal systems that could not be explained by biogeographic affinities. Because they live at depths where the environment is relatively uniform, many Non-migrators have broad distributions (Beamish et al., 1999), and the fronts do not seem to act as boundaries or sites of attraction for them. Consistent with these observations, the larval to adult ratio for the Non-migratory species was constant across all three frontal systems. Living at depths below the peak hydrographic gradients of the front, their populations appear to be largely unaffected by the processes above them at the scale that we studied. No studies we know of prior to Lara-Lopez et al. (2012) have investigated the differential response of Non-migratory mesopelagic fishes to fronts, and one of our most notable findings is that their density, assemblage composition, and larval indices were not influenced by the frontal features that we studied on the time and space scales examined.

Inshore and Frontal assemblages of both Migrators and Larvae were not statistically distinguishable from each other at either of the C- or E-Fronts. The C- and E-Front Frontal assemblages of both groups appear to be disproportionately derived from the coastal-associated assemblages (e.g., *L. stilius*, *L. ochotensis*, *T. crenularis*) with less contribution from oceanic taxa (e.g., *D. atlanticus*, *C. townsendi*). There is evidence that coastal water may be entrained into front-associated jets (Hood et al., 1990), and our results suggest that this water is accompanied by

coastal taxa, though we cannot distinguish whether this process may occur through active (i.e., behavior) or passive (i.e., transport) processes.

We detected differences in assemblages for Migrators at all fronts, and for Larvae at the A- and E-Fronts. As Migrators inhabit the epipelagic zone through their nocturnal excursions into surface waters and the Larvae reside in the epipelagic where environmental gradients associated with fronts are the strongest, their distributions are more directly affected by the presence of a front. Moser and Smith (1993) similarly found distinct larval fish assemblages across the Ensenada Front. The differences between the Northern and Southern assemblages at the A-Front were primarily based on biogeographic provinces (Lara-Lopez et al., 2012), while the assemblage at the E-Front were largely distinguishable by their oceanic or coastal associations. Most species collected at E-Front stations were found in both Offshore and Coastal/Inshore waters. Although mixing of assemblages occurred at all of the fronts, there is more similarity between regional assemblages at the C- and E-Fronts than for the A-Front (Figs. 4, 5, and 6). The A-Front may be a more permanent feature that behaves more like a barrier between the distinctive Subtropical and Subarctic-Transition Zone provinces (Moser and Smith, 1993; Chereskin and Niiler, 1994; Brodeur and Yamamura, 2005), while the more transitory eddy-associated C- and E-Fronts behave more as “blenders” (Bower et al., 1985; Sournia, 1994), with more subtle distinctions in the associated assemblages across the frontal zones. Still, we detected higher densities of warm-water species in the offshore region, and higher densities of coastal-oriented species in the nearshore, as would be expected.

The larval to adult ratio for Migrators as well as the larval assemblage compositions were unaltered at the C-Front, which we attribute to the dynamic nature of that frontal system (Brzezinski et al., 2015). The late-stage larvae that are effectively captured in the MOHT are at least 3–4 weeks old (Gartner and Brunswick, 1991; Moser, 1996), and were therefore spawned by adults living under different oceanographic conditions than at the time of our sampling. Younger larvae are smaller than our mesh size, and typically not retained. As several weeks are needed for larvae to accumulate at eddy-associated convergence zones (Olson and Backus, 1985), an increase in larval:adult ratios was not realized in this region.

There were, however, altered larval:adult ratios of Migrators across the more stable A- and E-Fronts. The patterns in larval indices at these two fronts are different, with higher values on the cooler, northern (more productive) side of the A-Front and on the offshore (less productive) side of the E-Front. Most of the larvae in this study are of species with larval durations from 20 to 70 days (Garner, 1991; Moser, 1996; Moku et al., 2001), a timespan that could be influenced by a persistent front. Bakun (2006) describes a tradeoff between better nutritional access and high growth potential in more productive (cooler) regions of fronts, and refuge from predation on the less productive side. Where the tradeoff results in higher growth potential depends on a number of factors, including predator densities and prey densities. We speculate that at the more southerly and offshore A-Front, there was lower overall predation on migratory larvae that allowed for the more productive Northern side to be the preferred habitat for spawning, while at the E-Front, there was enhanced survival in the Offshore region due to release from predation. Midwater oxygen concentrations are substantially lower on the colder sides of these fronts (Fig. 2a–d), with a particularly wide discrepancy at the E-Front, and it is possible that reproduction or larval survival at the Offshore side of that front is a response to increased larval survival in better-oxygenated waters. The response could also be attributed to nutrient depletion and reduced productivity that is known to occur within eddies (Gruber et al., 2011).

Although the differences were not significant, we did observe a tendency to higher larval to adult ratios of a number of species in both Southern and Offshore waters for both Subarctic-Transition Zone species and Subtropical species. *D. theta* are known to undergo spawning

migrations into subtropical waters (Moku et al., 2003; Sassa and Kawaguchi, 2004) despite their Subarctic-Transition Zone adult distribution, and our results suggest that a number of other species, such as *N. ritteri*, *B. wesethi*, and *I. antrostomus*, may employ a similar behavior (Figure S1). Our results may be confounded by sampling within two different seasons (Fall and Summer), as some species exhibit seasonal spawning (Moser, 1996).

There were a number of confounding factors in this study that hinder the ability to compare between these three systems. Trawling was conducted both by day and night. We did do some additional day-night comparisons (results not presented here), and found that combining daytime and nighttime sampling did not significantly alter results, likely because the Migrators were collected in similar abundances during deep daytime and shallow nighttime casts, and Non-Migrators were collected only during the daytime. Unfortunately, we could not control for seasonality based on cruise logistics. It is certainly possible that some of the differences we saw between the three systems were responses to season or variable ocean conditions (Miller et al., 2015) rather than differences in the frontal systems themselves. An additional confounding factor is that sampling occurred much deeper at the C-Front than at either the A- or E-Fronts. However we expect that this should mostly have affected the Non-migratory species, as they have generally deeper distributions. Larvae of most mesopelagic fishes exhibit ontogenetic migration from the epipelagic to the mesopelagic (Moser, 1996), and thus it seems unlikely that their sampling was biased by the different methodologies.

Incorporating data on predator density, water clarity, and patch density could inform the underlying mechanisms leading to our differential results in larval to adult ratios across the two different types of fronts. Our surveys did not sample water that was distant from the front (e.g., John, 2001), so it is difficult to say whether observed patterns, such as altered larval:adult densities on one side of a front, are a result of the association with the front or a result of association with the water mass itself. Future studies on the topic should compare not only the edge of the water masses adjacent to the front, but also non-front associated waters.

9. Conclusions

Through sampling of three different frontal systems within the southern CCE, this study builds upon the current understanding of the effects of pelagic fronts on mesopelagic fish assemblages. We found that within the CCE, there are different types of fronts – the more persistent East-West oriented feature that separates Northern and Southern water masses is associated with more distinct assemblages across its boundary than the more transient eddy-associated fronts. Living at depths beyond the influence of most of the front-associated gradients, the Non-migratory assemblage remained relatively uniform across frontal systems, while Migratory and Larval assemblages were altered by the presence of the front, likely because these groups respond more directly to the epipelagic gradients associated with the frontal systems. In the CCE, frontal frequency (Kahru et al., 2012) and upwelling (Sydeman et al., 2014) may be increasing, which could be a response to altered eddy activity (Strub and James, 2000). A key implication of our results is that fishes may benefit from the edge of fronts (Northern in the case of the E-W associated fronts, and Offshore in the case of the eddy-associated fronts) for reproduction and/or recruitment. This study shows that fronts can significantly alter the structure of mesopelagic communities, although frontal duration and location affect the magnitude of such changes. If the frequency of frontal occurrences in the southern CCE continues to increase, such features will likely differentially influence migratory and non-migratory mesopelagic fishes, through effects on the reproduction, survival, distributions, and predation on mesopelagic fishes.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at <http://dx.doi.org/10.1016/j.dsr.2018.03.005>.

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