Influence of internal bores on larval fish abundance and community composition

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H I G H L I G H T S

- A persistent, semi-diurnal internal tide occurs at the head of a submarine canyon.
 - The internal tide drives cold subthermocline waters (bores) onto the adjacent shelf.
 - Larval fish samples and bore activity are analyzed over a full year.
 - Along with seasonality internal bores are a key control on the larval fish community.
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A R T I C L E I N F O

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A B S T R A C T

A persistent semidiurnal internal tidal bore feature occurs at the head of the Monterey Bay Submarine Canyon and drives regular intrusions of cold, subthermocline waters onto the adjacent shelf. In this study, we examine the influence of this internal tidal bore feature on the larval fish community using over a year of periodic larval fish samples collected coincidentally with physical measurements. Larval samples were categorized into one of two water mass periods: a “warm period” representative of shallow coastal shelf waters and a “cold period” characteristics of colder waters present during internal bore forcing. Using multivariate statistical methods, we show warm and cold periods, along with seasonality, are the primary drivers of larval fish community composition. A significantly different community composition was observed between warm and cold water mass periods. This difference was primarily due to decreased abundance in most taxa during the cold periods, and did not indicate an obvious shift in the assemblage of the taxa. However, our data do indicate that some taxa may show higher abundance during cold periods compared to warm periods, but further studies are warranted. Along with seasonality, the presence/absence of subthermocline waters driven by internal bores appears to be a key control on nearshore larval fish community composition at this location.

1. Introduction

Early stage pelagic marine fish larvae and eggs are generally assumed to be limited in their ability to affect their location in the marine environment (Moser and Watson, 2006) and so, like many weak swimming larval forms, ocean currents are presumed to be the dominant driver of transport and subsequent patterns of distribution (Chia et al., 1984; Bradbury and Snelgrove, 2001). Behavior of late stage planktonic larvae may have a significant bearing on their distribution and abundance in the water column (Shanks, 2009; Shanks et al., 2003; Leis, 2006; Cowen and Sponaugle, 2009; Pineda et al., 2007) and so distribution may be partially uncoupled from transport mechanisms for these larvae; however,

even these larvae are still dependent on interactions with their environment (Morgan et al., 2009; Shanks, 1983; Pineda et al., 2007). The distribution and abundance of adult populations can also be affected by transport mechanisms that regulate the supply of juvenile recruits (Morgan et al., 2011; Raimondi, 1991; Sponaugle and Cowen, 1996). Describing processes that affect larval transport and abundance is therefore important in understanding community structure and population dynamics, and subsequently has a bearing on the management of marine resources such as fishery stock assessment, marine protected area design and management, and the strategic planning of ocean intake locations (Fogarty and Botsford, 2007; Hare and Walsh, 2007).

Larval dispersal and abundance are influenced by physical processes that act across a broad range of spatial and temporal scales (Gawarkiewicz et al., 2007; Bradbury and Snelgrove, 2001; Pineda et al., 2007). In eastern boundary current upwelling systems, such

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as the California Current, equatorward winds drive regional coastal upwelling. This seasonal process acts to drive deep, cold, and nutrient-rich waters close to the surface, thus fueling primary productivity (cf. [Walter et al., 2018](#)). Coastal upwelling also has the potential to generate and influence mesoscale features, such as ocean eddies, filaments, and persistent fronts (e.g., [Harrison et al., 2013](#); [Nidzieko and Largier, 2013](#); see [Chao et al. 2017](#) numerical model). At a regional scale, larval transport, abundance, and connectivity are most often associated with these mesoscale features ([Siegel et al., 2003](#); [Mitarai et al., 2009](#); [Bertness et al., 1996](#); [Kinlan and Gaines, 2003](#); [Watson et al., 2011](#); [Harrison et al., 2013](#); [Roughgarden et al., 1988](#)). On a smaller-scale and closer to the shoreline, larval transport and abundance are thought to be influenced by smaller-scale processes that drive cross-shelf exchange ([Pineda, 1994](#); [Mullineaux and Mills, 1997](#); [Cowen et al., 2007](#)), and this may influence larval abundance and distribution at these smaller spatial scales ([Shanks, 1983](#); [Shanks et al., 2014](#); [Pineda, 1994](#); [Vargas et al., 2004](#); [Liévana McTavish et al., 2016](#); [Woodson et al., 2012](#); [Nickols et al., 2013](#)).

There is an established body of evidence demonstrating that the supply of planktonic marine larvae to adult populations, in addition to other factors such as competition and predation that regulate adult population abundance and distribution patterns, can play an important role in the ecology of marine populations (e.g. [Connell, 1985](#); [Cowen, 1985](#); [Gaines et al., 1985](#); [Roughgarden et al., 1988](#); [Levin, 2006](#)). For fishes with sedentary adult stages, connectivity between patches of adults through larval dispersal is a major mechanism by which many marine taxa maintain population stability and persistence in the face of disturbance ([Hasting and Botsford, 2006](#); [Cowen and Sponaugle, 2009](#); [Burgess et al., 2014](#)), and factors such as physical processes that disrupt this connectivity can have important effects on patterns of adult distribution ([Woodson et al., 2012](#)). Indeed, many physical processes play an important role in determining patterns of larval abundance and ultimately the supply of settlement-competent larvae to adult habitats ([Gaylord and Gaines, 2000](#); [Roughgarden et al., 1988](#)). A better understanding of these processes will inform settlement and recruitment dynamics, as well as the distribution of adult populations ([Gaines et al., 1985](#); [Gaines and Roughgarden, 1987](#)).

This contribution examines the influence of a persistent, semidiurnal internal bore feature on the local abundance of marine larval fish over a complete annual cycle. Other studies have reported similar physical phenomena affecting the abundance and distribution of pelagic larvae at local scales ([Shanks, 1983](#); [Shanks et al., 2014](#); [Pineda, 1991, 1994, 1999](#); [Greer et al., 2014](#); [Liévana McTavish et al., 2016](#); and the references therein;). [Pineda \(1994, 1999\)](#) and [Liévana McTavish et al. \(2016\)](#) both demonstrated transport of larvae (fish and invertebrates) by internal tidal bores in a coastal environment. [Shanks \(1983\)](#) found that the pelagic larvae of an intertidal crab (*Pacygrapsus crassipes*) exploited tidally forced internal waves to transition onshore. Moreover, [Greer et al. \(2014\)](#) examined the role of internal waves in the fine-scale distribution of a broad assemblage of fish larvae and their predators. [Shanks et al. \(2014\)](#) correlated daily peaks in settlement of barnacle cyprids on the rocky intertidal with daily minimum temperatures over a 39-day period, and hypothesized that onshore transport was driven by the internal tide. This study examines the effects of internal bores on the assemblage and relative abundance of the larval fish community (cf. [Pineda, 1994, 1999](#); [Liévana McTavish et al., 2016](#); [Shanks, 1983](#); [Shanks et al., 2014](#)) across different seasons (cf. [Greer et al., 2014](#)).

In this study, we examine data from plankton tows collected over the course of more than a year alongside continuous physical measurements to examine patterns of larval fish abundance and composition in relation to a dominant oceanographic feature: a persistent, semidiurnal internal tidal bore ([Walter and Phelan,](#)

[2016](#)). The data presented here were collected as part of a wider observational study aimed at characterizing the physical and biological environment at the head of the Monterey Submarine Canyon (MSC) (cf. [Walter and Phelan, 2016](#)). As part of this project, [Walter and Phelan \(2016\)](#) documented the presence of semidiurnal tidal period pumping of cold-water masses from below the thermocline (subthermocline waters) onto the adjacent shelf at this location. These cold-water intrusions (internal bores) are the result of the interaction of the internal tide with the canyon edge and are the dominant mode of physical variability at this site. The internal bores resulted in large changes in temperature throughout the year with alternating cold (onshelf flow from the canyon advecting cold, subthermocline waters onto the shelf) and warm (offshelf flow back into the canyon returning shallow coastal shelf waters to the shelf) periods at the study site. Furthermore, the internal bores displayed a distinct seasonality, with increased semidiurnal temperature variance in the summer months during periods of strong regional upwelling favorable winds and the subsequent shoaling of the offshore thermocline. In contrast, during the winter months, the semidiurnal temperature variance decreased, with the occasional absence in bore activity, as the regional upwelling weakened and the offshore thermocline deepened. We refer the reader to [Walter and Phelan \(2016\)](#) for a more detailed description. We expand on this earlier work here and test the hypothesis that internal bores influence the larval fish abundance and composition at the head of the MSC.

2. Methods

Monterey Bay is a large, semi-enclosed coastal embayment featuring one of the largest submarine canyons on the west coast of the United States (MSC – [Fig. 1a](#)). This biologically diverse marine ecosystem is part of the Monterey Bay National Marine Sanctuary and features large commercial fisheries and some of the world's largest giant kelp forests (*Macrocystis pyrifera*). The intense productivity of Monterey Bay is partially driven by seasonal wind-driven coastal upwelling ([Pennington and Chavez, 2000](#)). Other physical conditions across the bay include a mixed semidiurnal surface tide, persistent upwelling jets and fronts, large amplitude internal waves, and nearshore internal bores (cf. [Shea and Broenkow, 1982](#); [Breaker and Broenkow, 1994](#); [Walter et al., 2012, 2014a, b, 2016](#); [Woodson et al., 2011, 2012](#); [Walter and Phelan, 2016](#); etc.).

The focus of this study is the head of the MSC, which terminates within a few hundred meters of the coastline ([Fig. 1b](#)). [Walter and Phelan \(2016\)](#) used depth averaged temperature signals and water current profiles measured at the canyon rim to demonstrate the semidiurnal exchange of two water masses: a warm, shallow water mass and a cool, subthermocline water mass (i.e., internal bore) advected onto the adjacent shelf. The same temperature data used by [Walter and Phelan \(2016; viz. the south mooring\)](#) to indicate the exchange of subthermocline and surface water bodies are used in this study. The temperature data were collected from a vertical array of five Onset Corporation HOB0 StowAway TidbiT temperature loggers (0.2 °C accuracy) sampling at 10 min intervals and spaced approximately 3 m apart in the water column (0.9, 4.0, 7.0, 10.1, 13.1 mab [meters above the bed]). Depth-averaged temperature from these thermistors are used to describe temperature dynamics given that there were minimal temperature differences in the vertical (see [Walter and Phelan, 2016](#)). The mooring collected temperature measurements nearly continuously from 9 March 2012 to 2 July 2013.

Plankton samples were collected from 14 separate surveys over a 12-month period from 21 June 2012 to 14 June 2013 ([Table 1](#)). For each survey, four distinct plankton tow samples, taken between 3 and 6 h apart, were collected from two locations (two samples

Fig. 1. (a) Bathymetry and topography of the Monterey Bay region. (b) Zoom in of the canyon head study site region indicating the location of the larval sampling sites I2 and I3 (blue circles) and oceanographic mooring (green circle). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

each at I2 and I3, Fig. 1b), resulting in 56 samples from the 14 surveys during the course of the year. Walter and Phelan (2016) used temperature data from an array of oceanographic moorings at several locations along the canyon rim to demonstrate that similar water mass properties and physical characteristics were observed along the canyon rim (i.e., larval sampling stations I2 and I3 experience the same water mass exchange). Surveys were typically sampled over a single 24-h period, encompassing both day and night periods; however, three surveys required resampling due to difficulty sampling when large jellyfish aggregations were present. All resampling occurred within time blocks no longer than 8 days (Table 1).

Plankton samples were collected according to the methods developed by the California Cooperative Oceanic Fisheries Investigations (CalCOFI) program (<http://calcofi.org/field-work/net-sampling.html>). Samples were collected using a standard bongo frame (c.f. CalBOBL method used by the CalCOFI program). This consisted of paired 0.71 m diameter openings each equipped with a 335 μm mesh plankton net, codend, and flowmeter (General Oceanics Model 2030R). Each flowmeter was mounted in the center of the bongo frame opening. A minimum target volume of 50 m^3 per net was collected for each sample. Vessel speed during sampling was maintained at less than 2 knots. The depth of the tows was determined by a real-time pressure sensor (KPSI Transducer 700 Series) transmitting through a coaxial tow line back to the research vessel through a 4–20 mA circuit. Samples were taken in oblique tow profiles (from the surface, to maximum depth, and back to the surface) and nets were fished to approximately 40 m below the surface at each of the two locations, once during the day and then once again at night. Upon retrieval of the nets from the water, all of the collected material was rinsed into the codend collection container and then transferred to glass jars and preserved with a 5%–10% solution of buffered formalin.

After at least 72 h, samples were placed in a solution of 70%–80% ethanol preservative in the laboratory. The collected material was examined under a dissecting microscope, and all fish larvae were removed and counted. After this, the organisms were placed in labeled vials and identified to the lowest possible taxonomic level. Fish specimens that could not be identified to the species level were identified to the lowest taxonomic classification possible. Due to the use of 335 μm mesh nets in the sampling instead of the

Table 1

Dates of plankton samples collected at two locations (I2 and I3) across 14 surveys during day and night. The water mass period classification is indicated by red circles (warm period) or blue triangles (cold period) for each individual sample.

Survey	Date	Day		Night	
		I2	I3	I2	I3
MLIA04	6/21/12	●	●	●	●
MLIA05	7/26/12			●	●
	8/2/12	▲	▲		
MLIA06	8/21/12	●	●	●	▲
MLIA07	9/21/12	▲	●	▲	●
MLIA08	10/25/12	●	▲	●	●
MLIA09	12/13/12	●	●	●	▲
MLIA10	1/17/13	●			
	1/24/13		●	●	●
MLIA11	2/11/13	▲	▲	▲	●
MLIA12	3/28/13	●	▲	●	●
MLIA13	4/11/13	▲	●	▲	●
MLIA14	4/25/13	●	●	●	●
MLIA15	5/8/13	▲	▲	●	
	5/9/13				●
MLIA16	5/28/13	▲	●	▲	●
MLIA17	6/14/13	▲	▲	▲	●

larger 500 μm mesh nets used by CalCOFI, some of the samples collected large volumes of zooplankton. Following Brewer et al. (1984) these samples were divided into smaller, more manageable subsamples using a Folsom plankton splitter. In these cases, aliquot portions of the original sample were obtained and sorted.

In order to examine the influence of the internal bore features on the abundance and composition of the pelagic larvae at this location, samples were categorized into one of two water mass periods, either a “cold period” or a “warm period”. The “warm period” represents shallow coastal shelf waters, while the “cold period” is indicative of the cold, subthermocline waters present during internal bore forcing.

Fig. 2. Identification of the warm and cold water mass periods. (a) One-day rolling standard deviation of the depth-averaged temperature used to identify periods of minimal bore activity. The bore activity threshold (standard deviation of 0.5°C) is highlighted by a dashed black line. (b) Time series over the entire record from 9 March 2012 to 2 July 2013 of the depth-averaged temperature (gray) and high-pass filtered (33 h) depth-averaged temperature (black). The dashed red lines in all three panels delineate individual larval sampling periods (56 total). Note that samples in panels (a) and (b) are difficult to differentiate during a single survey due to the long time series. (c) Zoom in of the MLIA16 survey highlighting the delineation of the four samples (red dashed lines) within the survey into warm (red “W”) or cold (blue “C”) periods.

The two water mass periods were identified as follows. Using the depth-averaged temperature, a one-day window rolling standard deviation (Fig. 2a) was calculated to identify periods of internal bore activity. This follows from the analysis of [Walter and Phelan \(2016\)](#) that utilized both a windowed standard deviation and wavelet analysis to assess the semidiurnal temperature variance over time and demonstrate periodic weakening in the intensity of the semidiurnal bore activity, particularly during the winter. A standard deviation threshold of 0.5°C was used to identify periods where, when below this threshold, temperature variations and water mass changes driven by internal bores were assumed to be minimal. This threshold accurately delineated periods of minimal bore activity, most frequently during the winter months (cf. [Walter and Phelan, 2016](#) and Fig. 2a). Major conclusions were not sensitive to small changes ($\pm 0.25^{\circ}\text{C}$) to this threshold. Samples collected during periods below this threshold (only 5 of the

56 samples collected) lacked significant temperature variability driven by the internal bore features and were therefore marked as “warm period” samples indicating the presence of shallow coastal shelf waters.

If significant temperature variations driven by bore activity were present (i.e., above the standard deviation threshold of 0.5°C), then it was necessary to delineate between the cold (onshelf flow from the canyon advecting cold subthermocline waters onto the shelf) and warm (offshelf flow back into the canyon returning shallow coastal shelf waters) periods of the bore at the study site (cf. [Walter and Phelan, 2016](#)). To differentiate between these two periods, the high-pass filtered (33 h half amplitude period) temperature was calculated (Fig. 2b) to isolate the influence of internal bores and remove lower frequency changes to the water column driven by, for example, upwelling/relaxation cycles ([Walter and Phelan, 2016](#)). Following this, samples collected during

Fig. 3. Concentration of larval fishes by sample for the ten most abundant taxa (by annual mean concentration) occurring in 4 or more samples. Bar shade corresponds to the water mass period at the time each sample was taken (cold period in blue or warm period in red). Taxa are abbreviated as follows: EM – *Engraulis mordax*, GL – *Genyonemus lineatus*, CIQ – CIQ goby complex, ULF – unidentified larval fish, LL – *Lepidogobius lepidus*, CS – *Citharichthys* spp., Myc – Myctophidae, BRF – blue rockfish complex, Osm – Osmeridae, SS – *Sardinops sagax*. Sample ID is coded as follows: survey (MLIA##), cycle (day or night; D or N respectively), site (I2 or I3). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

a time period when the temperature was greater than the high-pass filtered temperature were classified as warm period samples, while those that were less were classified as cold period samples (see example in Fig. 2c).

Samples collected during the warm and cold periods were analyzed using a multivariate approach to determine the effect of the internal bores on local larval fish community composition. A total of 56 samples were collected over the course of the study, which included 45 larval fish taxa. Two samples (one each from the cold and warm periods) contained no fish and were excluded from the multivariate analysis. In order to remove the effects of rare taxa from the multivariate analysis, taxa that occurred in fewer than four of the samples were not included (23 of the 45 taxa). The remaining 22 taxa from the 54 samples were transformed as the square root of the concentration to account for the large range among the abundances in the data (Clarke and Gorley, 2001). The transformed data were used to construct a Bray–Curtis dissimilarity matrix (Bray and Curtis, 1957). Differences in community composition could be

due to the assemblage (presence/absence) of taxa and the relative abundance of taxa. This matrix was used in a principal coordinate analysis (PCO) (Gower, 1966) to examine the patterns of variation among the samples. We opted for a PCO, rather than nonmetric multidimensional scaling (NMDS), since the coordinate axis scores from the PCO can be used as independent variables in additional analyses to explore relationships with other explanatory variables. The PRIMER analysis of similarities (ANOSIM) procedure was used to determine if a statistically significant difference using the Bray–Curtis dissimilarities could be detected between the samples classified into warm and cold periods (Clarke and Gorley, 2001). The relative contribution of individual species to the average similarity between samples within the two temperature periods was identified using the PRIMER similarity percentage (SIMPER) routine (Clarke and Gorley, 2001). The effect of the individual taxa on the average similarity between and within the two groups was calculated in SIMPER using a permutation routine on the original

Table 2

Mean concentration (larval fish per m³) of the most abundant larval fish (>99.9% cumulative abundance), ranked by annual average concentration, for warm period samples, cold period samples, and all samples combined for the study.

	Taxon	Warm (# per m ³)	Cold (# per m ³)	Annual average (# per m ³)	Cumulative percent concentration	Number surveys recorded
1	<i>Engraulis mordax</i>	0.356	0.109	0.268	48.8	12
2	<i>Genyonemus lineatus</i>	0.164	0.100	0.141	74.5	6
3	CIQ goby complex	0.046	0.008	0.032	80.3	13
4	Unidentified larval fish	0.032	0.014	0.026	85.1	12
5	<i>Lepidogobius lepidus</i>	0.020	0.005	0.015	87.8	9
6	<i>Citharichthys</i> spp.	0.012	0.004	0.009	89.4	8
7	Myctophidae	0.008	0.008	0.008	90.9	10
8	Blue rockfish complex	0.011	0.002	0.008	92.3	4
9	Osmeridae	0.009	None	0.006	93.4	8
10	<i>Ammodytes hexapterus</i>	0.004	0.006	0.005	94.4	1
11	<i>Sardinops sagax</i>	0.006	0.004	0.005	95.3	4
12	<i>Leptocottus armatus</i>	0.004	0.003	0.004	96.0	6
13	<i>Neoclinus</i> spp.	0.004	0.001	0.003	96.5	7
14	<i>Paralichthys californicus</i>	0.004	0.001	0.003	97.1	2
15	<i>Lepidopsetta bilineata</i>	0.001	0.005	0.002	97.4	4
16	<i>Parophrys vetulus</i>	0.001	0.004	0.002	97.8	3
17	Pleuronectidae	0.001	0.005	0.002	98.2	4
18	<i>Symphurus atricaudus</i>	0.001	0.004	0.002	98.5	3
19	<i>Artedius</i> spp.	0.001	<0.001	0.001	98.7	3
20	<i>Atherinopsis californiensis</i>	0.001	0.001	0.001	98.9	4
21	Bathymasteridae	<0.001	0.003	0.001	99.1	3
22	Cottidae	<0.001	0.002	0.001	99.3	5
23	<i>Lyopsetta exilis</i>	None	0.002	0.001	99.5	2
24	Pleuronectoidei	None	0.001	0.001	99.6	1
25	<i>Rhinogobiops nicholsi</i>	<0.001	0.001	0.001	99.8	3
26	KGB Rockfish complex	0.001	0.002	0.001	>99.9	3
Mean total density^a		0.693	0.298	0.552		
Mean taxa per sample^a		6.17	4.55	5.59		
Total taxa collected		41	30	45		

^a For each period (Warm and Cold) this is the sample mean for the year. For the Annual Average, this is the mean of the survey means.

data to recalculate the Bray–Curtis similarities among samples by sequentially excluding a single taxon from the calculations.

An analysis of variance (ANOVA) was conducted to test the null hypothesis that there was no significant difference in the abundance of all larval fish between cold and warm periods, controlling for variation throughout the year by including the surveys as blocks within the cold and warm period treatments. The ANOVA was run with no interaction term. The larval concentration data were right-skewed, so in order to meet the assumptions of ANOVA, several transformations were tested to achieve normally distributed model residuals. Transforms were tested by plotting histograms of the transformed data and quantile–quantile plots of the model residuals. A $\log_{10}(x + 0.01)$ transform, where x is the larval concentration for an individual taxon, demonstrated the best fit to a normal distribution of model residuals. Due to the unequal number of period conditions among surveys, Type II sums of squares were used to calculate the F statistic. Three of the surveys did not contain one of the period factors (see Table 1). These surveys were not included in the ANOVA model.

3. Results

3.1. General results

There were 7258 individual larvae in 45 taxonomic groups collected during the study. Three taxa comprised approximately 80% of the total average concentration of larvae across all of the samples (Table 2). These three taxa were northern anchovy (*Engraulis mordax*), white croaker (*Genyonemus lineatus*), and a complex of goby larvae identified as the CIQ goby complex. The three species in the CIQ goby complex are arrow goby (*Clevelandia ios*), cheekspot goby (*Ilypnus gilberti*), and shadow goby (*Quietula y-cauda*), which are indistinguishable from one another at the earliest larval stages (*Clevelandia*, *Ilypnus*, *Quietula* = CIQ goby complex). We do note, however, that shadow goby (*Q. y-cauda*) is a

southern California species and is not likely to occur as far north as Monterey Bay. Of the total average concentration of larval fishes collected, northern anchovy (*E. mordax*) constituted nearly 50%, white croaker (*G. lineatus*) more than 25%, and CIQ gobies more than 5%. The fourth most abundant taxon was unidentified larval fishes. This group, however, constituted slightly less than 5% of the total average concentration of larval fishes collected. The majority of these unidentified larval fishes were yolk sac larvae, which show little variation among species in the characteristics of their physical form. The remainder of the 10 most abundant taxa represented approximately 9% of the total average concentration of larval fishes collected.

The majority of larval fish collected (nearly 90% by concentration) were either yolk-sac or pre-flexion stage fish. Some taxa occurred during discrete seasons, while others occurred throughout the year (Fig. 3). Northern anchovy (*E. mordax*), CIQ goby, and unidentified larval fish (EM, CIQ and ULF, respectively, in Fig. 3) were collected in 12, 13, and 12 surveys, respectively, of the 14 total surveys. The second highest ranked taxon by annual average concentration was white croaker (*G. lineatus*) (GL in Fig. 3); however, it was collected in only six of the 14 surveys. These six surveys were consecutive (MLIA06 through MLIA11 — late-fall through mid-winter).

3.2. Warm and cold periods

Overall, the average density per sample of all larval fish taxa combined in the warm period samples (0.693 larvae per m³) was more than twice that of the cold period samples (0.298 larvae per m³) (Table 2). The average number of identified taxa collected in the warm period samples (6.17 taxa per sample) was also greater than the average number collected in the cold period samples (4.55 taxa per sample).

The first two PCO axes account for a total of 33.8% (21% and 12.8% for the first and second axis, respectively) of the variation

Fig. 4. First two coordinate axes from a principal coordinate analysis of the Bray–Curtis distances among the samples for the 22 most abundant taxa. Each point represents a sample collected during either a cold (blue triangle) or warm (red circle) period condition. The numeric values represent the month of the year each sample was collected. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

among the Bray–Curtis dissimilarities calculated using the samples for the 22 most abundant taxa (Fig. 4). The sample values for the first coordinate axis are strongly linked to the month of the year (Fig. 5). From April through August, 22 of the 27 samples collected in these months occurred below the center (i.e. <0) of this axis. All the samples collected in the remaining months occur above the axis center. The sample values on the second coordinate axis are strongly related to the cold and warm periods (Fig. 6). Warm period samples appear to cluster into two seasonally related groups in Fig. 4; spring-summer (April through August) and fall-winter (September through February). The cold period samples are more evenly spread throughout the PCO plot compared to the warm period samples, even though they have a smaller variance range and do not appear to show seasonally related clustering. The differences between warm and cold period samples, which align with the second PCO axis, are greatest during the spring-summer months (April through August, coinciding with the greatest internal bore activity, Walter and Phelan, 2016). These are spread from upper to lower left areas of Fig. 4. The fall-winter months (September through March) cluster more tightly to the upper right area in Fig. 4, suggesting less of an effect of the warm and cold periods (i.e., internal bores) on community composition during the winter period consistent with Walter and Phelan (2016).

A significant difference was detected between the warm and cold period samples using the ANOSIM routine ($p = 0.005$). ANOSIM analyses of the classification of samples using bore activity thresholds (i.e. windowed standard deviation) of 0.25 ($p = 0.007$) and 0.75 ($p = 0.003$) standard deviations were also significant indicating that small changes in the classification of samples did not affect the results of the test.

Ten taxa accounted for almost 80% of the total dissimilarity between the two groups calculated using the SIMPER routine (Table 3). The five taxa that contributed the greatest dissimilarity between warm and cold period samples also ranked as the five most abundant taxa on average throughout the year. The average densities of these, and most of the other taxa that contributed to the majority of dissimilarity between groups, were higher in the samples

Fig. 5. Scatter plot of the first principal coordinate axis plotted against month of the year. Each point represents a sample collected during either a cold (blue triangle) or warm (red circle) period condition. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Fig. 6. Boxplot of the distribution of the second principal coordinate axis scores by cold and warm period. The center lines of each boxplot show the median value of the second principal component. Upper and lower hinges are the 25th and 75th percentiles, respectively. Whiskers extend to the highest and lowest value within 1.5 times the inter-quartile range. Points outside this range are considered outliers.

collected during warm periods compared to cold periods (Table 2). The taxa that contributed the most to the dissimilarity between periods and were more abundant in cold period samples were English sole (*Parophrys vetulus*), rock sole (*Lepidopsetta bilineata*), California tonguefish (*Symphurus atricaudus*), sculpins (Cottidae), KGB (Kelp Gopher Black-and-Yellow) rockfish complex and right eye flounders (*Pleuronectidae*). The SIMPER analysis calculated a higher average similarity among the warm period samples (26.4%) compared to the cold period samples (18.9%), which supports the

Table 3

Results of the SIMPER analysis showing each taxon's absolute contribution and cumulative percentage contribution to the average Bray–Curtis dissimilarity of 80.8% between the warm and cold period groups. The table also includes taxa rank according to average annual abundance shown in Table 2.

	Taxon	Average dissimilarity	Cumulative contribution to dissimilarity	Abundance rank ^a
1	<i>Genyonemus lineatus</i>	0.1233	15.26%	2
2	<i>Engraulis mordax</i>	0.1070	28.50%	1
3	CIQ goby complex	0.0993	40.79%	3
4	unidentified larval fish	0.0764	50.24%	4
5	<i>Lepidogobius lepidus</i>	0.0646	58.24%	5
6	Osmeridae	0.0408	63.29%	9
7	<i>Sardinops sagax</i>	0.0339	67.49%	11
8	Myctophidae	0.0328	71.55%	7
9	<i>Leptocottus armatus</i>	0.0312	75.41%	12
10	<i>Citharichthys</i> spp.	0.0283	78.91%	6
11	Blue rockfish complex	0.0237	81.84%	8
12	<i>Parophrys vetulus</i>	0.0220	84.56%	16
13	<i>Neoclinus</i> spp.	0.0204	87.08%	13
14	<i>Lepidopsetta bilineata</i>	0.0202	89.58%	15
15	<i>Symphurus atricaudus</i>	0.0133	91.22%	18
16	Cottidae	0.0129	92.82%	22
17	KGB rockfish complex	0.0128	94.41%	26
18	Pleuronectidae	0.0123	95.92%	17
19	<i>Atherinopsis californiensis</i>	0.0102	97.18%	20
20	<i>Rhinogobiops nicholsi</i>	0.0095	98.36%	25
21	<i>Artedius</i> spp.	0.0071	99.24%	19
22	<i>Paralichthys californicus</i>	0.0061	100.00%	14

^a From Table 2.

results of the PCO showing greater seasonal clustering in warm compared to cold period samples.

Using ANOVA, a significant difference ($p < 0.001$) in the concentration of all larval fish taxa combined was detected between water mass periods, controlling for differences between surveys (seasonal variation). Concentration of larval fishes was greater in warm period samples compared with cold period samples for most surveys and this is reflected in consistently higher mean concentrations for warm periods compared to cold periods for each survey (Fig. 7). Two surveys, one in March and the other in May 2013, showed the opposite relationship, with higher mean concentrations in the cold period samples. Warm period means are otherwise consistently higher than cold period means (crosses in Fig. 7), despite the high variance among surveys.

4. Discussion

The physical environment at the head of the MSC is dominated by a semidiurnal, persistent internal bore feature that drives alternating cold and warm water periods (Walter and Phelan, 2016). The persistence of this semidiurnal exchange of water masses throughout the year allowed for the examination of this feature's effect on larval fish while controlling for the confounding effect of seasonal variation in abundance. The distribution of samples collected over a full annual cycle, stratified by approximately monthly survey blocks, allowed for a wide distribution of samples from both warm and cold periods. This in turn allowed for an examination of both seasonality and internal bore effects on larval fish abundance. In this study, the sampling was originally designed to gather information on average annual abundance. While the appearance of warm or cold period conditions was distributed throughout the year, the replicates for this factor were not orthogonal across seasonal (survey) blocks. Although this lowers the power of the statistical tests, the data do show a statistically significant influence of the different water mass periods on the abundance of larval fish. Notably, the average concentration of all larval fishes is significantly less in the samples collected during the cold periods compared with average concentration in the warm period samples, irrespective of the overall variation in concentration among surveys.

High variance in the abundance of larval fishes among surveys was observed (Figs. 3 and 7), indicating seasonal variation in larval abundances and composition throughout the year. In California, larval fish spawning is known to be concentrated in the winter (Moser and Watson, 2006), with nearshore assemblages shown to cluster into winter-spring (December–May) and summer-fall (June–November) assemblages, at least in southern California (Walker Jr et al., 1987; Gruber et al., 1982). Parturition in the genus *Sebastes* tends to occur later in the year with increased latitude (Moser and Watson, 2006) and these within-region trends are likely to occur within other fish groups. The primary source of detailed information on larval seasonality in the California biome is the CalCOFI program (Moser and Watson, 2006; Moser et al., 1993). However, the CalCOFI program focuses on oceanic sampling and some nearshore larval fish species are often rare or absent from these samples. Very few studies encompassing a full year of larval fish sampling have occurred nearshore in California, and those that have are almost exclusively located within southern California (Brewer et al., 1984; Barnett et al., 1984; Walker Jr et al., 1987). Subsequently, this is the first published account, to the authors' knowledge, that includes sufficient information to ascertain patterns of seasonal abundance in the Central Coast region of California.

Seasonal variation in community composition accounted for the largest amount of variance in the PCO of the Bray–Curtis distances (Figs. 4 and 5). During the fall-winter period (September through February), the community composition of larval fish species at this location is dominated by seasonally abundant white croaker (*G. lineatus*) and northern anchovy (*E. mordax*), with sanddabs (*Citharichthys* spp.) and some other less abundant taxa also peaking in abundance during this period (Fig. 3). These dominant species are reflective of similar data in Walker Jr et al. (1987) from southern California and of broad patterns of oceanic abundance (Moser et al., 1993), although offshore samples differ in the relative abundance of larval fishes of many deep water species such as myctophids and bathylagids. Rockfishes (*Sebastes*) also rank higher in abundance in oceanic samples than in nearshore samples (Moser et al., 1993). Among warm period samples, the community composition appears to cluster into a fall-winter community (September through February) and a spring-summer community (April through August)

Fig. 7. Concentration of all larval fishes (scales are $\log_{10}[x + 0.01]$ transformed) for each sample colored by period (blue circles for cold, red circles for warm). Solid circles show samples included in the ANOVA model. Empty circles are surveys missing one of the period factors. These samples were excluded from the linear model. Crosses represent the mean for each period and survey group included in the model. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

along the first PCO axis (Fig. 4). This pattern is less marked in the cold period samples. The fall-winter community cluster may be driven by these seasonally abundant taxa.

An order of magnitude difference in abundance occurred between the December survey (MLIA09) and the next most abundant survey in total larval fish. The large concentration of larval fishes observed in the December survey was not due to a single taxon, and so could not be accounted for as a local spawning event from a large school such as may occur with pelagic schooling fishes like northern anchovy (*E. mordax*). This observation and some of the other variation in abundance between seasonal (survey) blocks may be related to ecological factors acting on the larvae, such as predation and starvation. Physical processes separate from the internal bore field are another potential cause of variation amongst surveys. For example, weak to moderate winds may establish long parallel vortices at spatial scales of 10–100 m (i.e., Langmuir cells). These features concentrate plankton between alternating regions of small-scale downwelling and upwelling, resulting in local aggregations of species at these spatial scales (Langmuir, 1938). Coastal fronts have also been shown to aggregate plankton (Woodson et al., 2012; Wolanski and Hamner, 1988; Roughgarden et al., 1988; Wing et al., 1995; Ryan et al., 2014). Many of these features, particularly upwelling fronts, are seasonally persistent features that are modulated by upwelling/relaxation cycles and local diurnal wind forcing (Woodson et al., 2012; Walter et al., 2016, 2017). Other features, such as the propagation of internal waves and bores, can result in large pulses of concentrated plankton at discrete locations (e.g. Pineda, 1991, 1994, 1999; Shanks et al., 2014). While the aforementioned physical processes are known to affect local plankton distribution elsewhere, previous studies have demonstrated that the primary driver of physical variability

in water properties at this particular location is the internal wave and bore field (see Walter and Phelan, 2016 and the references therein).

Differences in the larval fish community composition for samples collected during warm and cold periods is reflected in the second PCO axis (Figs. 4 and 6). The ANOSIM results confirmed that there is a statistically significant difference in community composition between the two periods, and the SIMPER analyses indicates that the taxa collected in the warm and cold period samples were very similar. Furthermore, during the spring-summer months (first PCO axis values <0) the difference between the warm and cold periods appears to be greater than during the fall-winter months (Fig. 4 first axis values <0). Walter and Phelan (2016) showed that during the spring-summer upwelling season, the nearshore internal bore field is enhanced. This increased intensity of bore activity (evident in Fig. 2 as a seasonal increase in temperature variance) may explain these seasonal differences between cold and warm period samples in the PCO analysis and add weight to the evidence that the second PCO axis is a result of the effects of internal bore activity.

It is important to note that this study was not designed to resolve larval abundance patterns across the bore front, unlike the high spatiotemporal resolution sampling in Pineda (1994, 1999), Greer et al. (2014), and Liévana McTavish et al. (2016). However, similar to the Pineda (1994, 1999) studies, the warm water period samples in our study are characterized by a higher abundance of fish larvae. The evidence presented in this study indicates that similar dominant taxa occur in both water masses but that sub-thermocline water advected from the canyon by internal bores acts to decrease larval abundance at this location. It is plausible that a vertical gradient in spawning activity may be generating

Fig. 8. Difference between the average concentration in warm and cold period samples as a proportion of the average concentration for the entire survey for each taxa (Proportional Difference). Taxa are plotted according to their ranked average concentration for the entire survey (highest to lowest from left to right). Values above (below) zero have a greater average concentration in the warm (cold) period samples and have been filled red (blue). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

this effect, but further studies are needed to validate this particular mechanism.

We also note that larval behavior or physiology may influence the vertical distribution of larvae and the subsequent association with either of the two water masses. For example, the eggs and yolk sac larvae of sablefish (*Anoplopoma fimbria*), a deep water fish species, are found almost exclusively at depths >200 m, however later stage larvae migrate to the surface and are neustonic (Moser et al., 1994). Moreover, Ahlstrom (1959) demonstrated consistent patterns of vertical distribution in offshore larval fish community composition in relation to the thermocline, with several species showing distinctive affinities to water either above, below or within the thermocline. Other studies have described similar interactions between behavioral responses and physical processes that result in larval transport (Leis, 2006; Sponaugle and Cowen, 1996; Woodson and McManus, 2007). In this study, however, nearly 90% of the larval fish by concentration were either yolk-sac or pre-flexion stage larvae. These larval fish stages are not expected to exhibit behavioral responses to physical processes due to their premature developmental stage.

We did attempt to test the hypothesis that the subthermocline waters originating in the canyon may contain a distinct cold-water assemblage of larval fishes, as opposed to just a reduction in relative abundance. To better highlight the differences between warm and cold periods across taxa where large differences in absolute abundance occur, the difference in average concentration between the warm and cold periods was normalized as a proportion of the average concentration of all samples for each taxon in Fig. 8. Taxa above a proportional difference of zero contained a greater relative

abundance during the warm periods, while those below zero contained a greater relative abundance during the cold periods. The taxa are plotted according to their rank abundance (highest concentration to lowest concentration from left to right, respectively). The taxa appear to demonstrate three distinct groupings according to their rank abundance. The 14 most abundant taxa were typically more abundant in the samples during the warm periods than during the cold periods. This group included many pelagic and demersal species common to the nearshore shelf environment of Monterey Bay, such as northern anchovy (*E. mordax*), white croaker (*G. lineatus*), sanddabs (*Citharichthys* spp.), and neoclinid blennies (*Neoclinus* spp.). The two notable exceptions include myctophids (*Myxodiplosis*), a group of typically mesopelagic (deep water) fishes and Pacific sand lance (*Ammodontes hexapterus*), a typically shallow water species. Sand lance (*A. hexapterus*) occurred in only one survey and myctophids had the same mean abundance for both warm and cold periods. All other taxa in the 14 most abundant taxa were, on average, more abundant during warm periods than cold periods. The second grouping of taxa observed in Fig. 8, with abundances ranking from 15th to 27th, were typically more abundant in cold relative to warm period samples. This group of 13 taxa consists of six flatfish and several other benthic fishes including pygmy poacher (*Odontopyxis trispinosa*) and ronquils (*Bathymasteridae*). The third grouping with the lowest ranked abundances consists of taxa more common in warm period than cold period samples, although they are sampled in very low abundance.

In this case, deep water adult fishes may spawn offspring into the deep, cold-water mass, and therefore their larvae would cause a shift in assemblage in the cold-water period. There is some

evidence (for example Fig. 8) in this study that certain taxa demonstrate a higher abundance in the cold period (subthermocline waters), which may be due to the adult distributions and spawning patterns as described above. However, the SIMPER analysis points primarily to a reduction in abundance as dominating the change in composition observed in the multivariate analysis.

5. Conclusions

This paper documents the effects of a semidiurnal internal bore feature on the composition of larval fishes at the head of a submarine canyon. Along with seasonality, the local internal bore feature is an important control on the composition of the larval fishes at this site. Using multivariate statistical methods, significantly different community compositions were observed between warm and cold water mass periods driven by the internal bore forcing. These differences in composition were shown to be largely due to a change in absolute abundance and diversity. A significant reduction in the concentration of larval fishes occurred during cold periods of the internal bore, suggesting that the advection of subthermocline waters out of the canyon reduces larval fish concentrations at this location. Additionally, some evidence of a change in species assemblage associated with the exchange of the two water masses was present, but further studies are needed to verify this finding. This study was not originally designed to assess the effect of internal bores on the composition of larval fishes and subsequently, a non-orthogonal analysis was undertaken on the effects of the internal bore on larval fishes. For this reason, we were unable to statistically test the hypothesis that the different water masses contain distinctive assemblages of larval fishes, or that some taxa are indicative of either internal bore period. Future studies should focus on increasing the sampling intensity within the two water mass periods to obtain orthogonal replication within the experimental cells. While nonlinear internal waves and bores have been documented at other canyon and steep shelf locations worldwide (e.g., Petruncio et al., 1998 and the references therein; Hall et al., 2014 and the references therein), further studies of other nearshore canyon heads would be necessary to extend these results to other locations.

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