Dietary overlap and optimal prey environments of larval and juvenile sardine and anchovy in the mixed water region of the western North Pacific

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ABSTRACT: Studies on recruitment variability in Japanese sardine *Sardinops melanostictus* and Japanese anchovy *Engraulis japonicus* have focused on the mixed water region (MWR) and its southern waters in the western North Pacific. However, the availability of suitable prey for larval and juvenile sardines and anchovy in the MWR was poorly known. Here, we describe the feeding habits and prey environments of larval and juvenile Japanese sardine and Japanese anchovy in the MWR from 1970–2013, during a time of dramatic changes in sardine and anchovy stocks. Fish and zooplankton were sampled from April to July using a variety of nets. Larval and juvenile sardine and anchovy fed on similar prey, such as copepodites of calanoid (e.g. *Paracalanus* spp.) and poecilostomatoid (e.g. *Corycaeus affinis* and *Oncaea* spp.) copepods, except for between 1988 and 1991. The abundance of dominant copepod prey species varied with sea surface temperature, with *P. parvus* and *C. affinis* most abundant at approximately 16 to 17°C and *Oncaea* spp. at temperatures exceeding 20°C. Decreased abundance of *P. parvus* after 1988 coincided with poor sardine recruitment. Although larval and juvenile sardine and anchovy have similar diets in the MWR, temperature possibly affects the distribution and abundance of their prey, and consequently fish stocks in the Kuroshio-Oyashio ecosystem.

KEY WORDS: *Sardinops melanostictus* · *Engraulis japonicus* · Larvae · Juvenile · Feeding habits · Copepoda · Mixed water region · Kuroshio and Oyashio ecosystem

1. INTRODUCTION

Fluctuations in sardine and anchovy populations have occurred widely in the world's oceans (Alheit et al. 2009). Such population oscillations seem to be influenced by climate-driven oceanic environmental changes (Alheit & Bakun 2010, Kawasaki 2013, Nakayama et al. 2018). Of various hypotheses proposed to explain relationships between environmental variation and the population dynamics of sardines and anchovy, ocean temperature and prey availabil-

ity have been shown to influence the population dynamics and recruitment variability of these species. Fluctuations in ocean temperature explain population dynamics and recruitment of sardine and anchovy populations in the North Pacific (Noto & Yasuda 1999, Chavez et al. 2003, Takasuka et al. 2007, Lindegren & Checkley 2013, Lindegren et al. 2013) and the Humboldt Current System (Alheit & Niquen 2004). Variation in sardine and anchovy biomass was also influenced by the dominance of large-sized zooplankton such as eupahusiids (for anchovy),

and small zooplankton (for sardines) (Ayón et al. 2011). In the western North Pacific, Takahashi et al. (2009) described a positive relationship between the growth rates of Japanese sardine *Sardinops melanostictus* and Japanese anchovy *Engraulis japonicus* and copepod abundance. Variability in depth of the mixed layer in the frontal zone of the Kuroshio Extension during winter also affected the feeding conditions of sardine larvae in spring (Nishikawa et al. 2013a). However, the effects of prey availability on population dynamics and recruitment variability in sardine and anchovy have not been well examined, with studies on their early life stages being particularly limited.

Prey availability during early life stages is one of the main factors affecting fish recruitment variability (Houde 2008), with, for example, annual changes in the timing of plankton blooms and the abundance of preferred prey demonstrated to influence survival in the early life stages of fish (Beaugrand et al. 2003, Platt et al. 2003). Studies on the feeding ecology of fish larvae and juveniles have also revealed (for a variety of locations) prey selection is affected by the diversity of available prey taxa. (e.g. Sampey et al. 2007, Llopiz 2013, Okazaki et al. 2019). Thus, to examine how food availability in the early life stages of fishes can influence fish recruitment variability, the feeding habits of these larval and juvenile fish are best determined by identifying prey taxa at a fine taxonomic level.

In the western North Pacific, multi-decadal changes in Japanese sardine and Japanese anchovy stocks have been reported (Alheit et al. 2009). Maximum stock levels of Japanese sardine in the 1980s were followed by repeat recruitment failures between 1988 and 1991. Following collapses in stocks of Japanese sardine, stocks of Japanese anchovy increased in the 1990s. Sardine and anchovy spawning grounds are located mainly in the coastal waters off Japan, while larvae and juveniles can occur in both coastal waters and offshore areas like the Kuroshio Extension and mixed water region (MWR) (Checkley et al. 2009). Models have also demonstrated half of all particles released in spawning areas are transported eastward to the Kuroshio Extension, regardless of stock-related sardine spawning period and areas (Nishikawa et al. 2013b).

Although the abundance of larval sardines (post first-feeding) is unrelated to recruitment levels, successful recruitment requires late-larval and juvenile survival (Watanabe et al. 1995). A significant positive relationship between a recruit-per-spawning index and sea surface temperature (SST) in and south of the Kuroshio Extension was reported by Yatsu et al. (2005). Furthermore, growth rates of juvenile sardine and metamorphosing anchovy determine recruit abundances in the MWR (Takahashi & Watanabe 2004a, Takahashi et al. 2008). Therefore, variability in growth of metamorphosing and juvenile stages of Japanese sardine and anchovy in the Kuroshio Extension and MWR may be critical for recruitment.

Studies on the feeding ecology of larval and juvenile Japanese sardine and anchovy are largely limited to the coastal waters of Japan (e.g. Uotani 1985, Yasue et al. 2011, Yamamoto & Katayama 2012). These fishes feed mostly on crustaceans like copepods. The feeding habits of larval and juvenile sardine and anchovy in the MWR are less well known (Takagi et al. 2009), and were completely unknown until the 1990s. Unfortunately, the distribution of potential prey for larval and juvenile sardines and anchovy in the MWR is also poorly known. Recent research has suggested that an understanding of prey dynamics is key to understanding the population dynamics of sardine and anchovy in the North Pacific (Nakayama et al. 2018).

We describe the gut contents of early life stages of sardines and anchovy as well as the distribution of prey in the MWR between 1970 and 2013. During this period, dramatic alternations occurred in the proportional abundance of sardines and anchovy in the western North Pacific. Our objectives are to (1) compare the diets of larval and juvenile sardines and anchovy in the MWR, (2) identify any change in gut contents and dominant prey during this period, and (3) investigate patterns in the distribution of dominant prey taxa in relation to water temperature. Finally, we discuss the effects of trophodynamics on species alternations and stock sizes.

2. MATERIALS AND METHODS

2.1. Early life stages of fishes

Fish were sampled in the MWR in coastal waters off Japan to 169° E, from 34°–42° N, between April and July 1970–2013 (Fig. 1A). Larval and juvenile fishes were collected using a variety of nets during this time: from 1970–1995, they were caught using ring nets (1.3 or 2.0 m diameter, 500 μm mesh) towed at the surface; from 1996–2009, samples were collected by oblique tow (~30 m to the surface) using a Matsuda-Oozeki-Hu trawl net (5 m^2 opening, 1.59 mm mesh; Oozeki et al. 2004); and from 2010 to 2013 samples were collected by otter trawl (opening
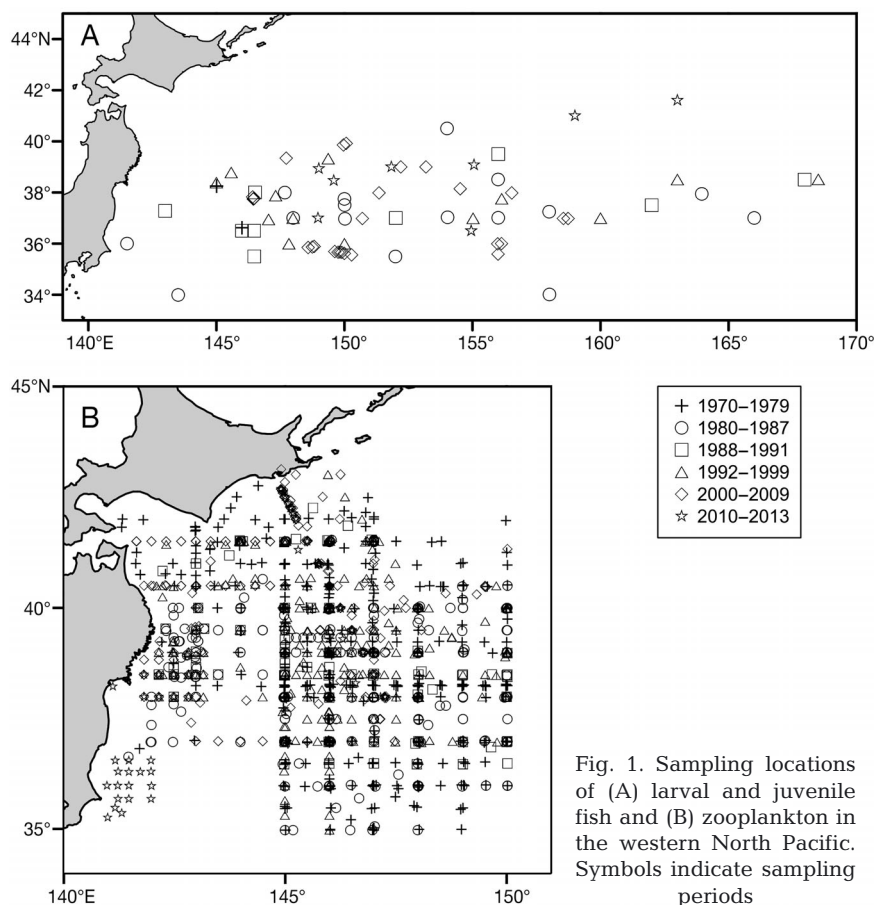
Fig. 1. Sampling locations of (A) larval and juvenile fish and (B) zooplankton in the western North Pacific. Symbols indicate sampling periods

analyses. Standard length (SL) was measured using digital calipers. Gut contents were identified to the lowest practical taxonomic level, and their prey length measured to the nearest 0.01 mm using a stage micrometer on a microscope. We define metamorphosing larval sardines as 20–31.9 mm SL and juveniles to be ≥32 mm SL (Matsuoka 2001), while those of anchovy were 20–36.9 mm SL and ≥37 mm SL, respectively (Takahashi & Watanabe 2004b). As day-collected fishes containing gut contents were limited in number, we pooled data into 6 sampling periods: 1970–1979, 1980–1987, 1988–1991 (sardine recruitment failure phase), 1992–1999, 2000–2009, and 2010–2013 (Table 1). These sampling periods reveal not only decadal trends in feeding and prey abundance in sardine and anchovy since the 1970s, but also their variability before and after the phase of sardine recruitment failure (1988–1991). We augment our gut content data with that of Takagi et al. (2009).

diameter ca. 27 m, 10 mm cod-end mesh) towed at the surface. Surface sea water for SST measurement was collected by lowering a bucket over the side of the ship at each station where larval and juvenile fishes were obtained.

Samples were preserved in 5 % buffered formaldehyde solution or 70 % ethanol. All larval and juvenile sardine and anchovy were sorted from net samples. Daytime-collected (sunrise to 3 h after sunset) larval and juvenile sardines and anchovy were used in

2.2. Zooplankton

Zooplankton in the MWR were collected from coastal waters to 150° E, 35°–43° N (Fig. 1B), using Maru-toku B (MTB), Norpac (NP), and Long Norpac (LNP) nets (0.45 m mouth-ring diameters, 330 or 335 μm mesh) towed at 150 m depth. The wire was retrieved at a speed of ~1.0 m s^{-1}. A total of 1572 samples were collected between April and July, from 1971 to 2013. Plankton samples were fixed and pre-

Table 1. Numbers and lengths of larval and juvenile Japanese sardine *Sardinops melanostictus* and anchovy *Engraulis japonicus* from the mixed water region by year. Data are mean ± SD. n: number of larvae or juveniles examined; SL: standard length (mm)

| | Sardine | | | | Anchovy | | | |
| | Larvae | | Juveniles | | Larvae | | Juveniles | |
	n	SL (mm)	n	SL (mm)	n	SL (mm)	n	SL (mm)
1970–1979	5	29.19 ± 0.76	2	40.43 ± 10.36	3	28.46 ± 1.85	3	47.82 ± 5.50
1980–1987	2	30.91 ± 0.71	65	57.91 ± 12.44	2	22.71 ± 1.90	0	
1988–1991	4	24.14 ± 2.46	17	48.32 ± 10.56	3	35.72 ± 1.40	21	40.97 ± 2.92
1992–1999	3	30.15 ± 0.19	49	43.57 ± 8.63	32	33.63 ± 3.22	17	40.87 ± 4.93
2000–2009	0		25	41.77 ± 5.65	35	26.28 ± 5.67	69	44.82 ± 6.12
2010–2013	0		116	62.79 ± 16.51	0		30	62.04 ± 10.52

served in seawater with 5% buffered formaldehyde solution. Adult copepods were identified to species, where possible. As not all net deployments had a flow meter, count data were not converted to abundance per volume or area. As the median value of filtering rates differed among nets (Takasuka et al. 2017), copepod count data from MTB, NP, and LNP nets were divided by filtering rate (0.751, 1.025, and 1.006, respectively) and then standardized to abundance per tow.

2.3. Data analysis

We express prey items in larval and juvenile sardine and anchovy gut contents as %N and %FO, where %N is the percentage of each prey category in the total number of prey categories, and %FO is the percentage frequency of occurrence of each prey item. We use group-average clustering to compare larval and juvenile sardine and anchovy prey over time. After counts of unidentified organisms (e.g. unknown crustacean fragments) in gut contents were removed from the data set, a criterion was set for the inclusion of prey taxa in cluster analysis: that a given prey taxa must be present in gut contents of >1% of larval and juvenile fish. As fish size influenced the number of prey items in gut samples, prey items were converted to % composition of total prey categories for each stage of each fish species before calculating a Bray-Curtis similarity matrix (Bray & Curtis 1957). Multivariate analyses were performed using PRIMER v.7 (Plymouth Marine Laboratory, Plymouth). Correlations between fish length and prey length, and differences in sardine and anchovy prey size distribution, were tested using the Pearson's correlation and the Kolmogorov-Smirnov test in R (v.3.31, R Core Team 2016), respectively. Our cluster analysis and the Kolmogorov-Smirnov test were performed only on data for sampling periods in which ≥15 larval or juvenile fish individuals were present.

To identify non-liner relationships between SST and abundances of 4 dominant prey copepods (*Paracalanus parvus*, *Corycaeus affinis*, *Oncaea mediterranea*, and *O. venusta*), we applied the Local Weighted Scatter Plot Smoother (LOWESS) using R. For time series analysis of dominant copepod prey, standardized abundance was calculated as follows:

$$\text{Standardized abundance} = (x - \bar{x})/\text{SD} \qquad (1)$$

where x represents an observed value, $\bar{x}$ represents the mean value during a sampling period, and SD is standard deviation. Standardized abundance was averaged for each sampling period. Because most

larval and juvenile fish gut content data were collected in May (63.6%) and June (31.6%), we used only copepod data for May (n = 384) and June (n = 475) in time series analysis.

3. RESULTS

3.1. Environment

SST at sites of fish collection varied between 11.3 and 21.5°C (Table 2), with an annual average between 15.1 and 18.7°C.

3.2. Diet and frequency of occurrence

Larval and juvenile sardines preyed mainly on copepods (e.g. *Paracalanus parvus*, immature *Paracalanus* copepodites, *Corycaeus affinis*, and *Oncaea venusta*) (Table 3), with juvenile sardines heavily preying on adult and immature *Paracalanus* copepodites (%FO: 73.7%), but with the %FO of *C. affinis* and *Oncaea* spp. also high. Larval and juvenile anchovy similarly preyed mainly on copepods, such as calanoids and poecilostomatoids, in addition to cladocerans, with the %FO of Cladocera, *Paracalanus* copepodites, *C. affinis* and *Oncaea* spp. all high.

3.3. Temporal variation in diet

Between 1970 and 1979, fishes fed mainly on copepods such as *Paracalanus* copepodites, *C. affinis* and *O. venusta*, but from 1980–1987, the diets comprised primarily immature *Paracalanus* copepodites (Fig. 2A–D). From 1988–1991, larval and juvenile sardine consumed calanoid copepods, such as copepodites of *Calanus* and *Paracalanus* (Fig. 2A,B), but anchovy ate mainly *Sapphirina* spp. and Thaliacea (Fig. 2C,D, 'Others'). From 1992–1999, larval and ju-

Table 2. Surface sea temperature (°C) by year over sampling period

| | SST (°C) | | Number of stations |
	Mean ± SD	Range	
1970–1979	16.0 ± 0.9	15.0 – 16.5	3
1980–1987	16.4 ± 1.4	13.6 – 18.9	16
1988–1991	15.1 ± 2.1	11.3 – 16.8	9
1992–1999	16.6 ± 1.7	14.2 – 19.7	12
2000–2009	18.7 ± 2.4	13.9 – 21.5	30
2010–2013	16.5 ± 1.8	12.2 – 18.4	10

Table 3. Japanese sardine *Sardinops melanostictus* and anchovy *Engraulis japonicus* gut contents. %N: percentage of each prey category in the total number of prey categories, %FO: percent frequency of occurrence of each prey item

Prey category	Sardine				Anchovy			
	Larvae		Juveniles		Larvae		Juveniles	
	%N	%FO	%N	%FO	%N	%FO	%N	%FO
Diplostraca								
Cladocera								
Evadne tergestina	3.8	7.1	<0.1	0.7	28.5	38.7	6.7	8.6
Other Cladocera	0.0	0.0	<0.1	2.9	37.3	36.0	1.7	7.9
Copepoda								
Calanoida								
Calanus immature copepodites	0.0	0.0	2.3	14.2	5.3	30.7	2.2	8.6
Clausocalanus parapergens	0.0	0.0	0.2	6.2	0.4	10.7	2.4	11.4
Clausocalanus spp.	5.5	7.1	0.1	6.2	0.6	18.7	0.2	9.3
Clausocalanus immature copepodites	3.3	7.1	0.3	8.4	0.2	4.0	0.3	5.0
Paracalanus parvus	8.5	64.3	21.8	62.4	1.7	22.7	2.4	33.6
Paracalanus immature copepodites	25.8	42.9	46.4	73.7	1.3	14.7	27.3	32.9
Calanoida copepodites	7.4	42.9	5.6	57.3	5.0	60.0	9.9	70.7
Cyclopoida								
Oithona spp.	0.3	7.1	0.1	6.6	0.5	10.7	0.9	11.4
Oithona immature copepodites	1.4	14.3	0.3	10.6	0.1	5.3	1.1	15.0
Harpacticoida								
Microsetella norvegica	0.5	7.1	0.1	6.9	<0.1	2.7	1.7	25.7
Harpacticoida copepodites	0.8	14.3	0.2	12.0	0.2	6.7	1.7	27.9
Poecilostomatoida								
Corycaeus affinis	6.6	21.4	3.6	59.9	5.1	45.3	11.6	59.3
Corycaeus spp.	0.5	7.1	0.2	9.5	0.2	8.0	0.4	12.1
Corycaeus immature copepodites	0.5	14.3	1.6	36.5	0.2	8.0	1.0	25.7
Oncaea media	0.0	0.0	0.0	0.7	1.9	30.7	0.8	15.0
Oncaea mediterranea	0.5	7.1	0.7	23.0	3.2	37.3	5.2	30.7
Oncaea scottodicarloi	3.8	7.1	0.6	21.9	2.8	40.0	4.2	47.1
Oncaea venusta	15.4	7.1	2.0	35.0	2.4	34.7	3.4	45.0
Oncaea waldemari	3.8	7.1	0.9	19.3	0.2	4.0	0.6	15.0
Oncaea immature copepodites	1.6	7.1	1.5	33.6	0.5	16.0	5.0	45.0
Poecilostomatoida copepodites	0.0	0.0	0.4	9.9	1.0	14.7	1.1	16.4
Unindetifed copepods	0.0	0.0	<0.1	1.1	0.2	8.0	0.4	7.1
Other prey items								
Krill furcilla	0.8	14.3	4.8	9.1	<0.1	1.3	4.2	10.0
Chaetognath	3.3	7.1	0.4	3.6	<0.1	1.3	0.2	2.9
Appendicularia house	0.0	0.0	1.3	9.5	0.0	0.0	0.2	3.6
Others	5.5	64.3	4.6	56.2	1.1	17.3	3.3	40.0

venile sardine and anchovy fed on calanoids and poecilostomatoid copepods (Fig. 2A–D), while anchovy also fed on Cladocera (Fig. 2C,D). From 2000–2009, both juvenile sardine and larval and juvenile anchovy consumed calanoid copepodites, *C. affinis*, *O. venusta*, and other copepodite copepods (such as *Oithona* spp. and *Microsetella* spp.) (Fig. 2B–D). From 2010–2013, juvenile sardine and anchovy ate *Paracalanus* copepodites and poecilostomatoid copepods (Fig. 2B,D).

Fig. 3 illustrates the %FO of dominant prey categories (*P. parvus*, immature *Paracalanus* copepodites, *C. affinis*, *O. mediterranea*, and *O. venusta*) over time. The %FO values tended to be low between 1988 and 1991, especially those for *P. parvus* and

their immature copepodites, which decreased during this period.

Cluster analysis (Fig. 4) reveals no difference in the diets of sardine and anchovy from 1992–1999, 2000–2009, and 2010–2013 (at 80% similarity level). However, the diets of these 2 fishes from 1988–1991 differed.

3.4. Prey size distribution between sardine and anchovy

Pearson's correlation analysis showed the regression between fish SL and log prey length to be signif-
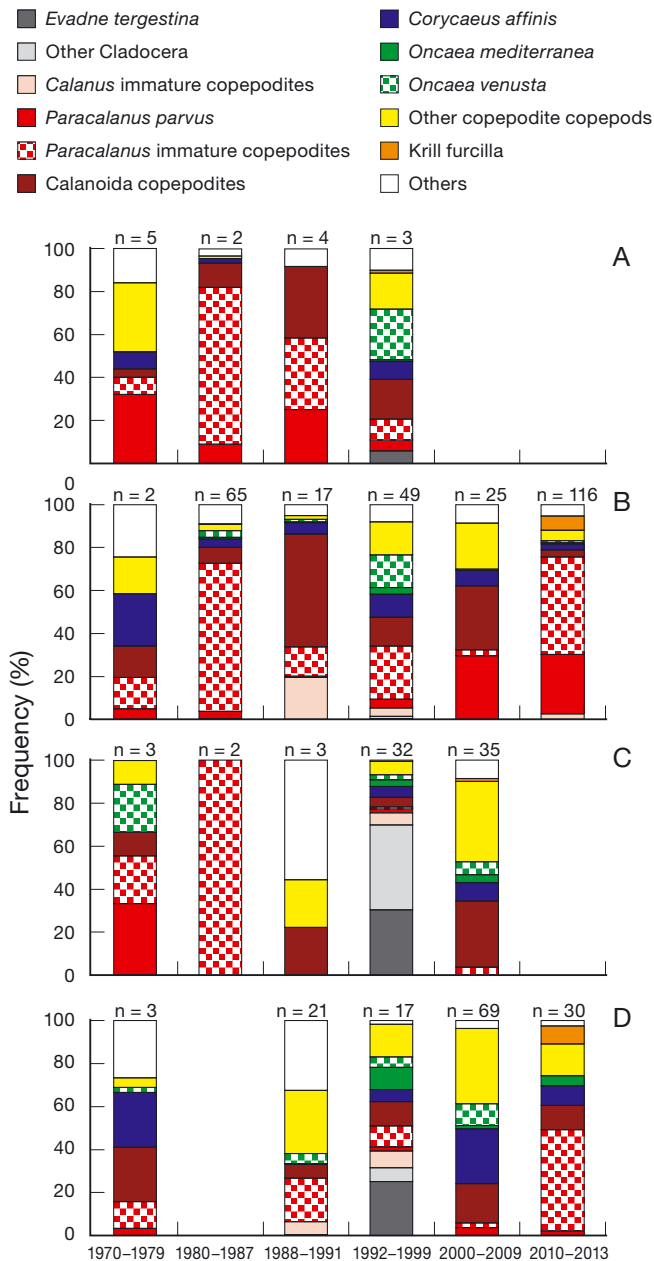
Fig. 2. Relative abundance of prey taxa in gut contents of sardine (A) larvae and (B) juveniles and anchovy (C) larvae and (D) juveniles, from 1970–1979, 1980–1987, 1988–1991, 1992–1999, 2000–2009, and 2010–2013. n: number of larvae and juveniles examined
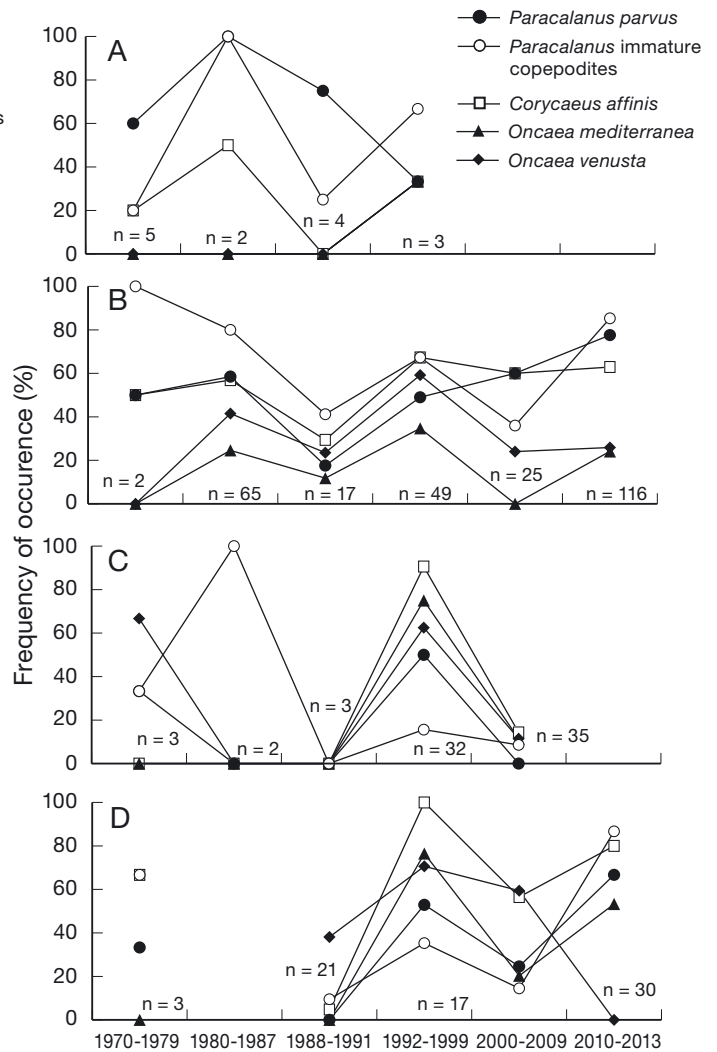

Fig. 3. Frequency of occurrence (%) of 5 dominant prey taxa in gut contents of sardine (A) larvae and (B) juveniles and anchovy (C) larvae and (D) juveniles, from 1970–1979, 1980–1987, 1988–1991, 1992–1999, 2000–2009, and 2010–2013. n: number of larvae and juveniles examined

icant, but the regression coefficient was quite low value (p < 0.05, r = 0.05) for sardine (Fig. 5A) and not significant (p = 0.10) for anchovy (Fig. 5B). Thus, for larval and juvenile fishes, there is unlikely to be a proportional increase in prey size relative to fish size. Significant differences in juvenile sardine and anchovy prey size (length) were not evident (Kolmogorov-Smirnov test, p > 0.05; Fig. 6).

3.5. Copepod prey

Abundance of copepod prey differed with SST (Fig. 7), with *P. parvus* and *C. affinis* most abundant around 16–17°C, and 2 *Oncaea* spp. (*O. mediterranea* and *O. venusta*) increasing when temperatures exceeded 20°C.

Fig. 8 depicts changes in the standardized abundance of 4 dominant copepod taxa over time. Copepod abundance varied over time, with, for example, that of *P. parvus* decreasing while *C. affinis* increased after 1988–1991, while that of 2 species of *Oncaea* did not change.
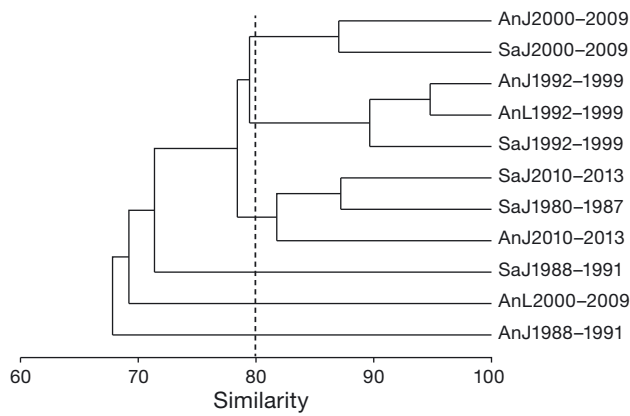
Fig. 4. Similarity of gut contents of sardine juveniles (SaJ) and anchovy larvae (AnL) and juveniles (AnJ), from 1980–1987, 1988–1991, 1992–1999, 2000–2009, and 2010–2013. Dashed line indicates 80% similarity level
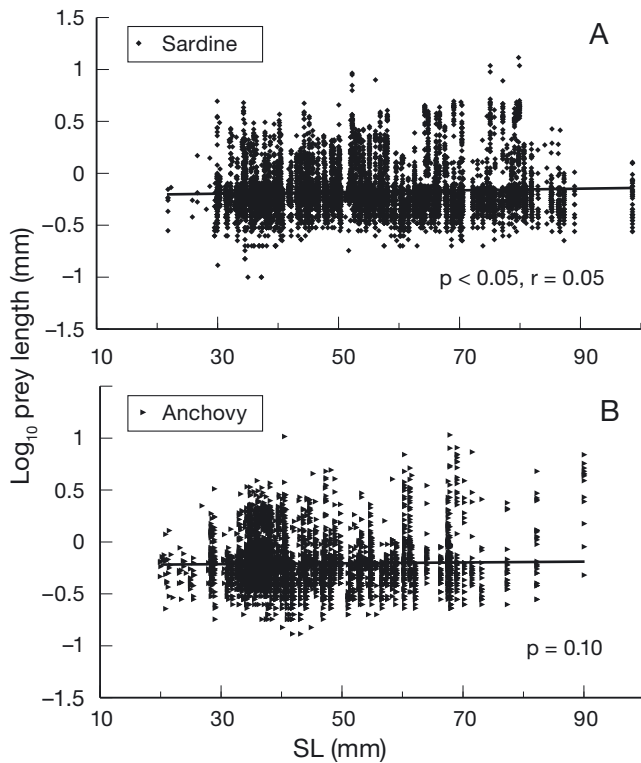

Fig. 5. Relationship between fish standard length (SL) and log-transformed prey length for larval and juveniles of (A) sardine and (B) anchovy. Black line: regression

Fig. 6. Frequency distribution of prey length in gut contents of (A–D) sardine and anchovy juveniles from 1988–1991, 1992–1999, 2000–2009, and 2010–2013. Bars: solid (sardine), open (anchovy). All values $p > 0.05$

4. DISCUSSION

Our results indicate the prey consumed by larval and juvenile sardines and anchovy was similar in the MWR (Table 3, Figs. 2 & 4). Gut content %N and %FO reveal *Paracalanus parvus*, immature *Para-calanus* copepodites, *Corycaeus affinis* and *Oncaea* spp. to all be important prey items for both fish species in this region. Calanoid copepods, such as *Para-calanus* spp., were previously identified as important in the diet of juvenile sardine and anchovy in this region as well (Takagi et al. 2009). In coastal waters
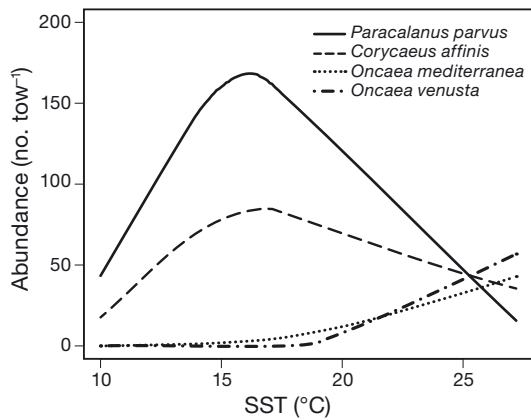
Fig. 7. Response plots for *Paracalanus parvus*, *Corycaeus affinis*, *Oncaea mediterranea*, and *O. venusta* in relation to sea surface temperature (SST) from Local Weighted Scatter Plot Smoother (LOWESS)
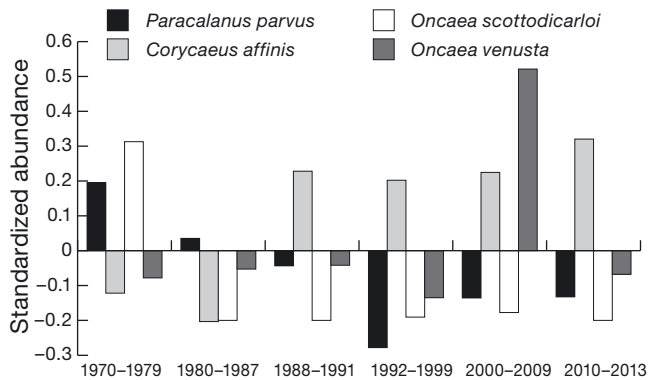

Fig. 8. Temporal change in standardized abundance of *Paracalanus parvus*, *Corycaeus affinis*, *Oncaea mediterranea*, and *O. venusta*, from 1970–1979, 1980–1987, 1988–1991, 1992–1999, 2000–2009, and 2010–2013

off Japan, sardine and anchovy larvae also feed on similar prey (Yasue et al. 2011, Yamamoto & Katayama 2012); stable isotopes have also identified trophodynamic similarities between them in the Kii Channel, southwestern Japan (Yasue et al. 2014).

Alternation in species over time has been attributed to differences in the trophic ecology of sardine *Sardinops sagax* and anchovy *Engraulis encrasicolus* in the Benguela ecosystem (van der Lingen et al. 2006). As the branchial apparatus of adult anchovy is relatively coarse, they are predominantly particulate-feeders that favor larger meso-zooplankton. As adult sardine have a relatively fine branchial apparatus, they are predominantly filter-feeders that favor smaller micro-zooplankton. Variations in the size structure of plankton communities induced by physical forces (e.g. wind) affect the prey environments of sardine and anchovy in the Benguela ecosystem. In

the Humboldt Current system, adult anchovy *Engraulis ringens* also preyed on larger items than adult sardine *S. sagax* (Espinoza et al. 2009), with fluctuation in their biomasses matching changes in the dominance of large-sized zooplankton (for anchovy), such as euphausiids, and small zooplankton (for sardines) (Ayón et al. 2011). In the Kuroshio-Oyashio ecosystem, variability in early survival rates was a key factor in the population dynamics of sardine and anchovy (Watanabe et al. 1995, Takahashi & Watanabe 2004a, Takasuka et al. 2007, Takahashi et al. 2008), and like these previous studies, we also found no marked difference in the prey of their larval and juvenile stages. The juvenile diets of another sardine, *Sardina pilchardus*, and anchovy *E. encrasicolus* in the Mediterranean Sea also did not differ significantly (Nikolioudakis et al. 2014). Thus, differences in the size of prey selected by sardine and anchovy are unlikely to explain the population dynamics of these species in the Kuroshio-Oyashio region.

Although sardine and anchovy consumed similar prey over time, their prey also changed over time. From 1980–1987 and 2010–2013, when sardine stocks were relatively large, sardine and anchovy fed mainly on *P. parvus* and immature *Paracalanus* copepodites. The contributions of *P. parvus* and *Paracalanus* copepodites to the diets of both species were relatively low between 1970 and 1979, 1988 and 1991, 1992 and 1999, and 2000 and 2009, which, with the exception of the period between 1970 and 1979, coincides with abundance of *P. parvus* in the environment (Fig. 8). Between 1988 and 1991, when sardine recruitment failed, the contribution of *Paracalanus* to the diets of both species, and in the environment, changed. Between 1988 and 1991, the diets of sardine and anchovy were more dissimilar than after 1992 (Fig. 4). Between 1988 and 1989, shifts occurred in SST and the Pacific Decadal Oscillation index in the North Pacific (Yasunaka & Hanawa 2002), which may have affected survival of early life stages of sardine and anchovy by affecting prey availability through changes in primary production and temperature.

To our knowledge, no ecological study has examined annual variation in the diets of early life stages of fishes over such a long period of time as that we report here. Although limited fish collections from the MWR, particularly before the 1990s, preclude our more fully determining relationships between diet, prey availability and sardine and anchovy stock size, we can demonstrate the importance of specific copepod prey in the diets of sardine and anchovy, as well as differences in prey distribution and abundance in this region over a long period of time. However,

given the variability in diet data for larval and juvenile fish, future research must evaluate the extent to which spatial and temporal variability in feeding habits within a year can influence inter-annual variation of prey availability on larval and juvenile fish.

Maximum abundances of *P. parvus* and *C. affinis* occurred from 16–17°C, while 2 *Oncaea* spp. were most abundant at temperatures exceeding 20°C (Fig. 7). In the Kuroshio ecosystem, *P. parvus* and *C. affinis* were prevalent in cooler coastal waters (Miyamoto et al. 2017), while *Oncaea* spp. were prevalent in the warmer Kuroshio Current and surrounding subtropical waters (Miyamoto et al. 2017). Our study, and that of Miyamoto et al. (2017), demonstrate that temperature likely affects the distribution of copepod prey throughout this region. Previous studies have argued that zooplankton biomass and size structure are key drivers of variation in the population dynamics of sardine and anchovy (Ayón et al. 2004, 2011). The copepods *P. parvus*, *C. affinis*, and species of *Oncaea* are generally small, and their distributions differ with temperature and between years. Further, changes in prey size relating to fish ontogeny, and differences in prey size between juvenile sardine and anchovy, were not evident (Figs. 5 & 6). These suggest zooplankton taxonomic composition, as well as zooplankton abundance and distribution, have a greater effect on the trophic ecology of sardine and anchovy in the Kuroshio and Oyashio ecosystems than zooplankton size might have. In terms of prey–predatory interactions, calculating a selectivity index would provide a better understanding of feeding availability of larval and juvenile sardine and anchovy. Unfortunately, as fish and zooplankton were not collected at the same time, location, or depth in this study, our data would not be appropriate to calculate a selectivity index for sardine and anchovy.

Although *P. parvus* and *C. affinis* occur at similar temperatures, *Paracalanus* are herbivorous particulate feeders (Paffenhöfer 1984, Suzuki et al. 1999), while species of *Corycaeus* are carnivorous (Landry et al. 1985). Not only is *P. parvus* capable of directly exploiting phytoplankton production, but its egg production rate is also positively correlated to chlorophyll *a* concentration (Uye & Shibuno 1992). Species of *Oncaea* consume discarded appendicularian houses (Ohtsuka & Kubo 1991, Nishibe et al. 2015) and marine snow (Kiørboe 2000). Annual variability in the winter mixed layer depth affects phytoplankton production in the northern Kuroshio the following spring (Nishikawa et al. 2013a), which may affect herbivorous copepod production (e.g. *P. parvus*). Therefore, variation in temperature and phytoplankton produc-

tion might contribute to spatial and temporal variability in larval and juvenile sardine and anchovy prey in the MWR. Although mechanisms affecting copepod population dynamics are not well understood in the MWR, climate-induced temperature and phytoplankton supply influenced size composition and biomass of copepods in the Kuroshio region (Nakata et al. 2001, Nakata & Hidaka 2003).

Larval sardine growth rates were greatest around 16°C (Takasuka et al. 2007). In the MWR, high abundances of *P. parvus* generally occurred between 16 and 17°C (Fig. 7), which likely affected the feeding and growth of larval and juvenile sardines. Peak growth rates of larval anchovy (at ~22°C; Takasuka et al. 2007) occur at temperatures higher than those associated with peaks described in *P. parvus* abundance but similar to those of 2 *Oncaea* sp. Abundances of *Oncaea* spp. were usually less than those of *P. parvus* (Fig. 7), indicating larval and juvenile anchovy might not encounter high prey abundance at those temperatures that promote their optimum growth.

As temperature affects larval growth and the distribution and abundance of copepod prey, an optimal growth temperature hypothesis might explain a sardine-anchovy regime shift (Takasuka et al. 2007). Temperature-correlated variation in copepod abundance might reflect variation in primary production caused by physical forces, such as winter mixing strength and mixed layer depth change (Nishikawa et al. 2013a). Possible interactions between temperature, growth, and sardine and anchovy prey abundance are depicted in Fig. 9. When temperature is low and larval and juvenile sardine prey are abun-
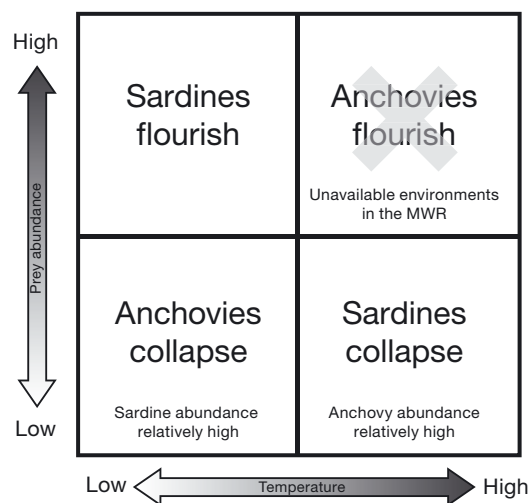

Fig. 9. Relationship between temperature, prey abundance, and sardine and anchovy survival in the mixed water region (MWR)

dant, sardine growth rate and stocks will be high. Conversely, when temperatures are high and larval and juvenile anchovy prey are abundant, anchovy growth rate and stocks will be high. When temperatures are high and larval and juvenile sardine prey are not abundant, sardine growth rates and stocks will decrease relative to those of anchovy.

As high abundances of major prey species like *Paracalanus* spp. were seldom encountered in high-temperature environments (~22°C) in the MWR (Fig. 7), it is unlikely that larval and juvenile anchovy would encounter abundant prey. Moreover, anchovy would not flourish at lower temperatures, because their larval growth is temperature-dependent (Takasuka et al. 2007), even if food was abundant. However, temperatures optimal for growth and abundant prey for larval and juvenile sardine were encountered in this region. Therefore, interactions between physiological responses (i.e. growth) and prey availability for larval and juvenile fish in environments experiencing variable temperature might lead to species alternations and changes in population size.

Landings of sardine in the western North Pacific are an order of magnitude greater than those of anchovy (Oozeki et al. 2019). Although no evidence for an effect of temperature or prey availability on larval and juvenile stages was reported by Oozeki et al. (2019), Peruvian anchovy biomass dominated in a low-temperature, high-zooplankton-biomass regime (Ayón et al. 2004), and differences in sardine and anchovy spawning temperature optima were reported for the Kuroshia-Oyashio system and California Current systems (Takasuka et al. 2008). As alternation in the proportional abundance and landings of sardine and anchovy are also reported for the California and Humboldt Currents system (Alheit et al. 2009), our hypothesis could be tested in ecosystems other than the Kuroshia-Oyashio environment.

Recent studies have demonstrated the importance of interspecies interactions (Nakayama et al. 2018, Takasuka et al. 2019) and intraguild predation (Irigoien & De Roos 2011) on the population dynamics of small pelagic fish. Accordingly, it is important to understand relationships between food resource availability and prey–predator interactions. For this reason, we report the feeding habits, and the abundance and distribution of copepod prey, of larval and juvenile sardine and anchovy in the MWR. Although the early life stages of sardine and anchovy probably do not have discrete diets in the MWR, temperature does affect optimal prey environments, which may then affect populations of sardine and anchovy in the Kuroshio-Oyashio ecosystem.

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