In this study, historical data available since 1954 were used to get new insight to ontogenetic and spatiotemporal variability in Peruvian anchovy or anchoveta *Engraulis ringens* diet. Whatever the period, *E. ringens* foraged mainly on macrozooplankton and the importance of euphausiids in *E. ringens* diet appears directly related to euphausiids abundance. This bottom-up effect is also observed at smaller scale because the euphausiids fraction increased with *E. ringens* total length and euphausiids accessibility. Selecting the largest prey, the euphausiids, provides an energetic advantage for *E. ringens* in its ecosystem where oxygen depletion imposes strong metabolic constraints on pelagic fishes. This study illustrates the plasticity of *E. ringens* that allows it to cope with its highly variable environment.

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Key words: euphausiids; Humboldt Current system; oxygen; Peruvian anchovy; spatiotemporal variability; trophic ecology.

**INTRODUCTION**

The Peruvian anchovy, or anchoveta, *Engraulis ringens* Jenyns 1842 is the dominant pelagic nekton species in the coastal Northern Humboldt Current system (NHCS) off Peru. This fish has great ecological importance in channelling energy flow from primary and secondary production to higher trophic levels (Pauly *et al.*, 1989). For decades *E. ringens* was considered to depend mainly on phytoplankton (Ryther, 1969; Rojas de Mendiola, 1989; Alamo & Espinoza, 1998). These studies were based on counts of *E. ringens* prey, a method considered to be inadequate for estimating dietary importance (James, 1987; Konchina & Pavlov, 1995). By applying an analytical method based on the estimation of prey carbon content, Espinoza & Bertrand (2008) showed that *E. ringens* forage mainly on macrozooplankton, in particular euphausiids and large copepods. Such trophic behaviour is common for *Engraulis* spp. (van der Lingen *et al.*, 2009).

*Engraulis ringens* diet may have changed over time. Indeed, the *E. ringens* population was assumed to be dominated by individuals with higher affinity for
zooplankton (shorter guts and fewer gillrakers) during the 1950s and 1960s than after the *E. ringens* collapse in 1972 (Palomares *et al*., 1987; Hutchings, 1992). An opposite change could have occurred in the last decades explaining the strong dominance of zooplankton in *E. ringens* diet observed by Espinoza & Bertrand (2008). To check for this historical trophic diet data available since 1954 were revisited.

To complete previous work, the feeding behaviour of *E. ringens* according to fish total length (*L*<sub>T</sub>) (ontogenetic), and spatial (latitudinal and cross-shore) and diel patterns during the 1996–2003 period derived from available data are described.

**MATERIALS AND METHODS**

**DATA**

The study area covers the Peruvian coastal waters from the coastline to c. 200 km offshore. In Peru, the manner data have been acquired and analysed (*i.e.* quality) has changed with time. In order to study both long-term changes and spatial variability, available appropriate data were used.

The oldest data covering the period 1954–1969 were collected at different seasons in several processing plants for *E. ringens*: (1) Chimbote (9° S) in August to December 1954 (69 stomachs) and in January to December 1955 (333 stomachs); (2) San Juan (15° S) in April and June 1969 (64 stomachs); (3) Mollendo (17° S) in March 1954 (26 stomachs), January and April 1963 (24 stomachs) and March and June 1969 (27 stomachs); and (4) Ilo (17.5° S) in April 1954 (11 stomachs) (Rojas de Mendiola, 1971). Individuals of *E. ringens* were randomly sampled and fixed in 10% formalin. Stomach content items were identified and counted, taking as a unit for zooplankton at least the head and the whole cell for phytoplankton. Prey data from Rojas de Mendiola (1971) (counts) were converted into carbon content by applying the methodology described in Espinoza & Bertrand (2008). Prey data expressed as carbon content were pooled into the following six taxonomic categories: (1) diatoms, (2) other phytoplankters, (3) calanoid copepods, (4) other copepods, (5) euphausiids and (6) other zooplankters. No latitude and longitude was available for these data.

For the period 1974–1988 data were retrieved from EUREKA operations; these employ about 20 fishing boats for a quasi-synoptic observation of the Peruvian coast and fish resource monitoring. The specific determination of trophic items was coarse and did not allow for a comprehensive diet analysis, but the frequency of occurrence of euphausiids in stomach content could be estimated. The same information was obtained from samples collected during scientific surveys or from fish processing plants in 1985, 1988–1990, 1994, 1995 and 2004–2009 (Table SI, Supporting Information).

Data for the period 1996–2003 were collected on board research vessels of the Peruvian Sea Institute (IMARPE) during 22 acoustic surveys (Table I). The samples and the methodology used for stomach content analysis and conversion to carbon were described in Espinoza & Bertrand (2008). A total of 13 430 fully georeferenced stomachs of *E. ringens* were used. The prey data were pooled into the same six taxonomic categories as for the period 1954–1969. The data were also pooled for: *L*<sub>T</sub> class, latitude, distance to the shelf break and diel period (Table II). Seasonal variability was not considered because no significant effects were found (Espinoza & Bertrand, 2008).

**ANALYSES**

From these data sets, and taking into account their characteristics, three kinds of analyses were performed. (1) *Engraulis ringens* diet was compared between 1954–1969 and 1996–2003. Interannual variability was not used because the first data set was based on only few samples of some years while the second has already been described by Espinoza & Bertrand (2008). (2) A time series of the frequency of occurrence of euphausiids between 1954 and 2009 was constructed. (3) The fully spacialized data set from 1996 to 2003 that allowed
studying ontogenetic and spatial variability in *E. ringens* diet was used. Given that ANOVA assumptions for the data were not met (lack of normality), the non-parametric Kruskal–Wallis (KW) test (Scherrer, 1984) was used to identify statistical differences in the carbon content-based contribution of different prey taxa according to the factors: $L_T$ class, latitude, distance to the shelf break and diel period. A Tukey-type test was used for *a posteriori* multiple comparisons (Zar, 1999). Finally, classification and regression trees (CART; Breiman *et al.*, 1984) were used to assess the relative importance of $L_T$, latitude, distance to the shelf break and diel period on *E. ringens* diet. This non-parametric method uses a partitioning algorithm to estimate a series of binary decision rules that divide the data optimally into smaller homogeneous subgroups. The whole dataset is represented by a single node at the top of the tree. Then the tree is built by repeatedly splitting the data. Each split is defined by a simple rule based on a single explanatory variable. Splits are chosen to maximize the homogeneity of the resulting two nodes. Each terminal node (or leaf) of the final tree is characterized by a predicted prey distribution (carbon proportion for the six taxonomic groups), given the explanatory variables. For pruning the tree and validating the robustness of the CART results the recursive partitioning method (rpart; De’ath & Fabricius, 2000) was used.

RESULTS

TEMPORAL VARIATION


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**Table I.** Year, start and end date, number of trawls, number of stomachs with prey contents and total length ($L_T$) range of *Engraulis ringens* during 1996–2003

<table>
<thead>
<tr>
<th>Year</th>
<th>Start date</th>
<th>End date</th>
<th>Number of trawls</th>
<th>Number of stomachs (with prey)</th>
<th>$L_T$ (cm) (range)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1996</td>
<td>10 February</td>
<td>1 April</td>
<td>49</td>
<td>157 (147)</td>
<td>11.0–18.5</td>
</tr>
<tr>
<td></td>
<td>16 November</td>
<td>19 December</td>
<td>39</td>
<td>338 (329)</td>
<td>9.5–19.0</td>
</tr>
<tr>
<td>1997</td>
<td>13 February</td>
<td>23 April</td>
<td>45</td>
<td>186 (184)</td>
<td>10.5–19.5</td>
</tr>
<tr>
<td></td>
<td>4 September</td>
<td>5 October</td>
<td>51</td>
<td>117 (106)</td>
<td>11.5–18.5</td>
</tr>
<tr>
<td>1998</td>
<td>27 March</td>
<td>1 May</td>
<td>35</td>
<td>148 (124)</td>
<td>10.0–17.0</td>
</tr>
<tr>
<td></td>
<td>23 August</td>
<td>17 September</td>
<td>36</td>
<td>348 (308)</td>
<td>4.0–15.0</td>
</tr>
<tr>
<td>1999</td>
<td>30 November</td>
<td>21 December</td>
<td>36</td>
<td>274 (232)</td>
<td>4.0–16.0</td>
</tr>
<tr>
<td></td>
<td>14 February</td>
<td>28 March</td>
<td>75</td>
<td>1197 (1059)</td>
<td>10.0–17.0</td>
</tr>
<tr>
<td></td>
<td>28 August</td>
<td>17 September</td>
<td>19</td>
<td>279 (178)</td>
<td>10.0–18.0</td>
</tr>
<tr>
<td></td>
<td>12 November</td>
<td>14 December</td>
<td>70</td>
<td>1243 (999)</td>
<td>8.0–18.0</td>
</tr>
<tr>
<td>2000</td>
<td>20 January</td>
<td>26 February</td>
<td>124</td>
<td>1965 (1798)</td>
<td>6.5–18.5</td>
</tr>
<tr>
<td></td>
<td>10 June</td>
<td>6 July</td>
<td>50</td>
<td>928 (859)</td>
<td>7.5–18.5</td>
</tr>
<tr>
<td></td>
<td>28 August</td>
<td>23 September</td>
<td>38</td>
<td>512 (486)</td>
<td>7.0–18.5</td>
</tr>
<tr>
<td></td>
<td>11 October</td>
<td>13 November</td>
<td>45</td>
<td>822 (717)</td>
<td>6.5–18.0</td>
</tr>
<tr>
<td>2001</td>
<td>3 March</td>
<td>10 April</td>
<td>78</td>
<td>1584 (1446)</td>
<td>8.5–18.5</td>
</tr>
<tr>
<td></td>
<td>5 July</td>
<td>6 August</td>
<td>83</td>
<td>1274 (1208)</td>
<td>6.5–19.0</td>
</tr>
<tr>
<td>2002</td>
<td>21 February</td>
<td>18 March</td>
<td>83</td>
<td>1362 (1094)</td>
<td>7.0–18.0</td>
</tr>
<tr>
<td></td>
<td>10 August</td>
<td>31 August</td>
<td>30</td>
<td>269 (267)</td>
<td>9.5–17.0</td>
</tr>
<tr>
<td></td>
<td>1 October</td>
<td>13 November</td>
<td>36</td>
<td>415 (365)</td>
<td>10.0–17.0</td>
</tr>
<tr>
<td>2003</td>
<td>26 February</td>
<td>31 March</td>
<td>45</td>
<td>524 (513)</td>
<td>6.5–17.5</td>
</tr>
<tr>
<td></td>
<td>16 August</td>
<td>15 September</td>
<td>26</td>
<td>243 (237)</td>
<td>7.5–17.5</td>
</tr>
<tr>
<td></td>
<td>24 October</td>
<td>10 December</td>
<td>36</td>
<td>798 (774)</td>
<td>4.5–17.5</td>
</tr>
</tbody>
</table>
zooplankton; the contribution of phytoplankton represented only 0.8% of the diet expressed as carbon (Fig. 1). Euphausiids contribution was >92.3%, more than during 1996–2003 when the mean euphausiids contribution was 67.5%. The copepod fraction was also lower during 1954–1969 (6.3%) than during 1996–2003 (26.3%).

The frequency of occurrence of euphausiids varied with time (Fig. 2). Even if the time series is incomplete, a pattern emerged with fewer euphausiids during the mid-1970s and mid-1980s (available data: 1974–1979, 1985, 1988 and 1989) and maybe during the 1950s. In this last case, the data (available data: 1954–1955) are insufficient to provide robust results. On the other hand, euphausiids were more frequent during the late 1960s to early 1970s and the late 1990s to early 2000s. This pattern is similar to what was observed by Ayón et al. (2011) who studied the temporal changes in zooplankton dominant $L_T$ groups (between small, medium and large zooplankton, and euphausiids) in net samples. Euphausiids dominance in zooplankton from Ayón et al. (2011) matches the frequency of occurrence of euphausiids in *E. ringens* diet (Fig. 2), except during the mid-2000s when euphausiids dominance increased while the frequency of occurrence in stomachs decreased.

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**Table II.** Factors used to pool the data

<table>
<thead>
<tr>
<th>Factors</th>
<th>Classes</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Engraulis ringens</em> $L_T$ class (cm)</td>
<td>By 2 cm size class: [4–6&gt;, [6–8&gt;, [8–10&gt;, [10–12&gt;, [12–14&gt;, [14–16&gt;, [16–18&gt;, [18–20&gt;</td>
</tr>
<tr>
<td>Latitude ($\degree$S)</td>
<td>By degree of latitude from 03$\degree$30’ S to 18$\degree$ S</td>
</tr>
<tr>
<td>Distance to the shelf break (km)</td>
<td>Negative inshore, positive offshore: $&lt;-30$, $-30$ to 0, 0 to 30, &gt;30</td>
</tr>
<tr>
<td>Diel period</td>
<td>(i) 0700 hours $\leq$ day $&lt;$ 1700 hours</td>
</tr>
<tr>
<td></td>
<td>(ii) 1700 hours $\leq$ dusk $&lt;$ 1900 hours</td>
</tr>
<tr>
<td></td>
<td>(iii) 1900 hours $\leq$ night $&lt;$ 0500 hours</td>
</tr>
<tr>
<td></td>
<td>(iv) 0500 hours $\leq$ dawn $&lt;$ 0700 hours</td>
</tr>
</tbody>
</table>

$L_T$, total length.
Fig. 2. Frequency of occurrence (%F₀, N) of euphausiids in *Engraulis ringens* stomachs, and euphausiids dominance from Ayón et al. (2011) in zooplankton net samples (additive model results, −). No bar indicates the absence of data.

**ONTOGENETIC VARIATION**

Across all *Lₜ* classes the contribution of zooplankton to *E. ringens* diet in terms of carbon content was ≥ 95% [Fig. 3(a)]. For all *Lₜ* classes the most important prey groups were euphausiids and calanoid copepods, but their relative importance varied significantly with *E. ringens* *Lₜ* (KW test, *P* < 0.001, Table III; Tables SII, SIII and SIV, Supporting Information). The most noticeable pattern was the steady increase in euphausiids contribution with *E. ringens* *Lₜ* [Fig. 3(a)]. Euphausiids represented 23-3% of the diet of the smallest *E. ringens* (4–6 cm *Lₜ*) but reached 84-9% for the largest (18–20 cm *Lₜ*). At the same time the proportional contribution of calanoid copepods markedly decreased from 68-0% in the smallest *Lₜ* class of *E. ringens* to 11-5% in the largest. The proportion of other zooplankters also diminished with increasing *Lₜ*, but not as regularly, from 8-8% in the smallest to 2-0% in the largest *E. ringens*. The contribution of other phytoplankters remained below 0-6%, and other copepods under 2-5% without a clear trend at each *Lₜ* class. For diatoms, their contribution increased from 0-1% in the smallest *Lₜ* class to 4-4% for the 10–12 cm *Lₜ* class and then diminished to <1% in the larger *Lₜ* classes.

**TABLE III.** Results of non-parametric ANOVA (Kruskal–Wallis test); *n* = 1938 (the 13 430 stomachs pooled by total length, *Lₜ*, class)

<table>
<thead>
<tr>
<th>Items</th>
<th><em>Lₜ</em> class, d.f. = 7</th>
<th>Latitude, d.f. = 15</th>
<th>Distance to the shelf break, d.f. = 3</th>
<th>Diel period, d.f. = 3</th>
</tr>
</thead>
<tbody>
<tr>
<td>Diatoms</td>
<td><em>H</em> = 60.5, <em>P</em> &lt; 0.001</td>
<td><em>H</em> = 47.7, <em>P</em> &lt; 0.001</td>
<td><em>H</em> = 73.0, <em>P</em> &lt; 0.001</td>
<td><em>H</em> = 16.7, <em>P</em> &lt; 0.001</td>
</tr>
<tr>
<td>Other phytoplankters</td>
<td><em>H</em> = 53.1, <em>P</em> &lt; 0.001</td>
<td><em>H</em> = 51.3, <em>P</em> &lt; 0.001</td>
<td><em>H</em> = 22.6, <em>P</em> &lt; 0.001</td>
<td><em>H</em> = 14.2, <em>P</em> &lt; 0.01</td>
</tr>
<tr>
<td>Calanoid copepods</td>
<td><em>H</em> = 24.2, <em>P</em> &lt; 0.001</td>
<td><em>H</em> = 44.4, <em>P</em> &lt; 0.001</td>
<td><em>H</em> = 10.1, <em>P</em> = 0.018</td>
<td><em>H</em> = 80.5, <em>P</em> &lt; 0.001</td>
</tr>
<tr>
<td>Other copepods</td>
<td><em>H</em> = 35.8, <em>P</em> &lt; 0.001</td>
<td><em>H</em> = 49.5, <em>P</em> &lt; 0.001</td>
<td><em>H</em> = 11.0, <em>P</em> = 0.012</td>
<td><em>H</em> = 64.2, <em>P</em> &lt; 0.001</td>
</tr>
<tr>
<td>Euphausiids</td>
<td><em>H</em> = 94.7, <em>P</em> &lt; 0.001</td>
<td><em>H</em> = 84.1, <em>P</em> &lt; 0.001</td>
<td><em>H</em> = 115.6, <em>P</em> &lt; 0.001</td>
<td><em>H</em> = 72.5, <em>P</em> &lt; 0.001</td>
</tr>
<tr>
<td>Other zooplankters</td>
<td><em>H</em> = 31.0, <em>P</em> &lt; 0.001</td>
<td><em>H</em> = 111.8, <em>P</em> &lt; 0.001</td>
<td><em>H</em> = 36.8, <em>P</em> &lt; 0.001</td>
<td><em>H</em> = 20.1, <em>P</em> &lt; 0.001</td>
</tr>
</tbody>
</table>
**LATITUDINAL VARIATION**

The contribution of zooplankton to *E. ringens* diet was ≥ 95% irrespective of latitude [Fig. 3(b)]. Euphausiids and calanoid copepods varied significantly with latitude (KW test, $P < 0.001$, Table III; Tables SV, SVI and SVII, Supporting Information) but no steady latitudinal trend was observed. Euphausiids were the main taxa with the exception of around latitudes 7° and 15° S where the most important prey were calanoid copepods, with 52.3 and 47.5%, respectively. The higher contributions of other zooplankters were observed close to Chicama (7° S) and south of San Juan (16° S) with 7·3 and 8·7%, respectively. The contribution of diatoms fluctuated between 0·04% in the extreme north to a maximum of 4·40% at 6° S with no apparent latitudinal trend [Fig. 3(b)].

**CROSS-SHORE VARIATION**

Euphausiid contribution varied significantly according to distance to the shelf break [Fig. 3(c), KW test, $P < 0.001$, Table III; Tables SVIII, SIX and SX, Supporting Information]. It steadily increased from 45% in the more inshore samples to reach 80% at >30 km from the shelf break. Contribution by calanoid copepods followed an opposite trend with the highest contribution (46%) in the more inshore samples then a decrease to 15% at >30 km from the shelf break. The contribution of other zooplankters was highest in the more inshore areas (7·6%) and varied between 2·0 and 4·1 further offshore. Finally, the collective contribution of diatoms, other copepods and other phytoplankters was marginal with <1·3% of carbon content in all cases.

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**DIEL VARIATION**

*Engraulis ringens* diet [Fig. 3(d)] showed significant differences with the diel period (KW test, $P < 0.001$, Table III; Tables SXI, SXII and SXIII, Supporting Information). At night, the diet was dominated by euphausiids (80.2%). This proportion decreased to 48.8% at dawn and 52.7% during the day, and reached a minimum of 39.8% at dusk. Calanoid copepods followed an opposite trend with 15.7% during the night, 35.3% at dawn, 40.9% during the day and 46.5% at dusk.

**CART ANALYSIS**

Results of the CART (Fig. 4) confirmed the above but permitted the ranking of effects as: distance to the shelf break $>$ diel period $>$ latitude $>$ $LT$ $>$ year. When looking at the tree (Fig. 4), the first cut is due to the distance to the shelf break with more copepods very close to the coast. Further to the coast, the second cut was related to $LT$ with more euphausiids in fish $>14$ cm. For fish $<14$ cm, copepods were more important at specific latitudes ($4^\circ$, $6^\circ$, $7^\circ$, $8^\circ$, $10^\circ$, $11^\circ$, $12^\circ$ and $15^\circ$ S), in particular during all diel periods other than the night.

**DISCUSSION**

**TEMPORAL VARIATION**

The quality of available data strongly varied with time. The use of different data sources allows for a better vision of the temporal changes in *E. ringens* diet. Results complete the one from Espinoza & Bertrand (2008) and show that the diet of *E. ringens* in Peru is based primarily on large zooplankters whatever the period (Fig. 1). Euphausiid contribution was even higher during the 1950s–1960s (92.6%) than during the late 1990s to early 2000s (67.5%), whereas copepods presented an opposite trend (6.3 and 26.3%). Euphausiids frequency of occurrence time series shows (Fig. 2) that euphausiids incidence decreased during the mid-1970s and mid-1980s. This trend is in agreement with the study of temporal changes in zooplankton size-group dominance by Ayón et al. (2011) who showed that euphausiids were strongly dominant during the late 1960s to early 1970s (the 1950s were not included in their analysis) and since the 1990s.

**ONTOGENETIC CHANGES**

Both juvenile and adult *E. ringens* were largely zooplanktivorous and foraged predominantly on euphausiids and calanoid copepods, while contribution of phytoplankton to dietary carbon was $\leq 4.4\%$ irrespective of $LT$ class. This is in contrast to that of Rojas de Mendiola (1969) and Rojas de Mendiola et al. (1969) who applied the numerical method and proposed that *E. ringens* become more phytoplanktivorous from juvenile to adult. Prey-size range, however, changed ontogenetically with a steady increase in euphausiids contribution from $>25\%$ in the smallest *E. ringens* (4–6 cm) to $>80\%$ in the largest $LT$ class (18–20 cm). For *Engraulis* spp., filter feeding has a high metabolic cost compared to particulate feeding (James
& Probyn, 1989; van der Lingen et al., 2006) and *E. ringens* select the largest available prey (Espinoza & Bertrand, 2008). Energetically, oxygen matters. Indeed, fishes need sufficient amounts of both food and oxygen, but the latter might be more difficult to obtain than the former (Pauly, 2010). This is particularly the case in the NHCS, which encompasses an intense and shallow oxygen minimum zone and where, close to the coast, even surface waters are undersaturated in oxygen (Bertrand et al., 2011). In this system, oxygen appears as an important driving factor of small pelagic fish populations and the availability of large prey such as euphausiids provides an energetic advantage to *E. ringens* compared with sardine *Sardinops sagax* (Jenyns 1842) (Bertrand et al., 2011). This study supports this contention because *E. ringens* appear to select the largest available prey they can capture. Indeed, the progressive change in diet composition with fish size can be attributed to the predator’s ability to capture and handle the prey, which is reflected by the size range of

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Fig. 4. Classification and regression tree of *Engraulis ringens* diet according to the spatiotemporal factors from 1996 to 2003: distance of the shelf break (dsb), latitude (lat), total length (*L_T*) class (size) and diel period (period). Each terminal node of the tree is characterized by a dominant prey. The predicted prey distribution (carbon proportion) for the six taxonomic groups is shown. Euphausiids (Euph), calanoid copepods (Cala), other copepods (Oth.Cop.), other zooplankton (Oth.zoo), diatoms (Diat) and other phytoplankton (Oth.phyt).
prey it can capture (Crowder, 1985; Christensen, 1996; Lundvall et al., 1999). The upper size limit of prey is set by physical constraints of the predator, in particular mouth gape (Hart & Hamrin, 1988), swimming capacity (Christensen, 1996; Lundvall et al., 1999) and its visual acuity and reaction distance to prey, which also increases with increasing predator size (Breck & Gitter, 1983). During ontogenetic shifts in $L_T$, *E. ringens* have thus greater access to larger and more energetic prey such as euphausiids.

Such ontogenetic changes in diet were observed in the other species of anchovies: *Engraulis mordax* Girard 1854 in California (Leong & O’Connell, 1969; O’Connell, 1972), *Engraulis encrasicolus* (L. 1758) in South Africa (James & Findlay, 1989), the north-west Mediterranean Sea (Tudela & Palomera, 1997; Plounevez & Champalbert, 2000) and the Bay of Biscay (Plounevez & Champalbert, 1999) and *Engraulis anchoita* Hubbs & Marini 1935 in Argentine (Ciechomski, 1967; Viñas & Ramírez, 1996).

This ability to adapt to varying conditions was defined as dietary flexibility (James & Findlay, 1989). This can be expressed within the foraging theory framework as a way to optimize the prey intake which provides high energy at low energetic and oxygen cost and in turn can be digested and avoid intraspecific and interspecific competition (Griffiths, 1975; Pyke, 1984; Werner & Gilliam, 1984). The calanoid copepods size ingested by *E. ringens* fluctuated between 0.65 and 4.0 mm, whereas the mean size of the euphausiids was estimated as 12 mm (Espinoza & Bertrand, 2008). These differences in prey size imply that *E. ringens* display two feeding strategies: filtering on the smaller copepods and biting on the larger prey. Such behaviour has been described in *E. mordax* in California (Leong & O’Connell, 1969; O’Connell, 1972) and *E. encrasicolus* (formerly known as *Engraulis capensis* Grant & Bowen, 1998) off South Africa (James & Findlay, 1989), the north-west Mediterranean Sea (Tudela & Palomera, 1997; Plounevez & Champalbert, 2000) and the Bay of Biscay (Plounevez & Champalbert, 1999). The threshold for the shift from filtering to biting was estimated as 0.7 mm for *E. encrasicolus* (James & Findlay, 1989) and 1.5 mm for *E. mordax* (Chiappa-Carrara & Gallardo-Cabello, 1993).

**SPATIAL AND DIEL CHANGES**

The zooplanktonic fraction dominated *E. ringens* diet irrespective of latitude, refuting the contention of a latitudinal-dependent dietary shift of *E. ringens* being more zooplanktivorous in the south and phytoplanktivorous in the north of Peru (Rojas de Mendiola, 1971; Pauly et al., 1989).

Interestingly, if euphausiids dominated *E. ringens* diet all along the coast, calanoid copepods dominated at 7° and 15° S and were relatively abundant at 4°, 7° and 10°–12° S [Fig. 3(b)]. At these latitudes the contribution of diatoms was also higher. In fact, by latitude, calanoid copepods were significantly correlated to diatoms ($r^2 = 0.50$, $P < 0.001$). These areas are known to have active upwelling (Morón, 2000), with 7° and 15° S corresponding to strong upwelling at Chicama and San Juan. In such areas the upwelled cold coastal waters are advected far from the coast and disperse coastal productivity, including zooplankton from the shelf into the offshore domain (Keister et al., 2009). The abundance of diatoms and small non-vertically migrating zooplankton is usually higher within an upwelling area than outside (Keister et al., 2009).
The present results also question a previous assumption according to which *E. ringens* forage more on phytoplankton inshore and zooplankton more offshore (Rojas de Mendiola & Ochoa, 1973; Pauly *et al.*, 1989). Indeed, the zooplankton fraction dominated *E. ringens* diet irrespective of the distance to the shelf break. Nevertheless, calanoid copepods were three times more abundant in stomachs sampled in the more inshore station than those sampled at >30 km from the shelf break [Fig. 3(c)], while the larger zooplankton items, *i.e.* the euphausiids strongly dominated the diet offshore. This pattern matches the cross-shore distribution of macrozooplankton off Peru with larger and more abundant zooplankton offshore than inshore (Ballón *et al.*, 2011). Also, in the samples, *E. ringens* $L_T$ increased with the distance to the coast. In particular, no *E. ringens* <10 cm were observed at a distance from the coast >160 km. Both larger fish and higher availability of large prey offshore explained the observed patterns. Similar results have been observed on *E. encrasicolus* and *Engraulis japonicus* Temminck & Schlegel (1846), which feed on smaller prey inshore than offshore, following the trend in fish size distribution (Plounevez & Champalbert, 1999; Tanaka *et al.*, 2008).

Within its coldwater coastal habitat, *E. ringens* is able to forage efficiently across a range of temporal, spatial and thermal scales (Espinoza & Bertrand, 2008). A clear diel pattern appears from the *E. ringens* diet results, with euphausiids reaching 82% during night hours while copepods accounted for c. 40% during other diel periods [Fig. 3(d)]. Such patterns fit with the diel vertical migration of macrozooplankton (Ballón *et al.*, 2011). Indeed, *E. ringens* are restricted to the surface oxygenated water (Bertrand *et al.*, 2008, 2010, 2011). During the day it has little access to the bulk (c. 79%) of the macrozooplankton community that is distributed within the oxygen minimum zone (Escribano *et al.*, 2009; Ballón *et al.*, 2011). The portion of macrozooplankton that stay in the upper layer during the day is mainly composed of small-sized sub-adult and juvenile euphausiids, and large copepods (Ayón *et al.*, 2008; Ballón, 2010; Ballón *et al.*, 2011). Similar patterns were observed in *E. encrasicolus* in the southern Benguela Current system (James, 1987).

In summary, *E. ringens* take the bulk of its energy from zooplankton, in particular euphausiids and copepods. This is irrespective of the period, *E. ringens* $L_T$, distribution and diel period. During the last decades, the importance of euphausiids in *E. ringens* diet appears directly related to euphausiids abundance and not to physiological factors as assumed previously (Hutchings, 1992). This bottom-up effect is also observed at smaller scale because the euphausiids fraction increased with *E. ringens* $L_T$ (concurrent with the capacity of *E. ringens* to capture and handle the larger prey) and euphausiids accessibility (*e.g.* higher offshore and at night). Selecting the largest prey, the euphausiids, provides an energetic advantage for *E. ringens* in its ecosystem where oxygen depletion imposes strong metabolic constraints to pelagic fishes (Bertrand *et al.*, 2011). Finally, this study is another illustration of *E. ringens* plasticity (Espinoza & Bertrand, 2008), which allows it to cope with the highly variable NHCS environment.

The authors gratefully thank the ‘Laboratorio de Ecología Trófica’ staff from the Instituto del Mar del Perú (IMARPE) for having facilitated the use of the data. T. Miller is warmly thanked for English editing and useful comments. A. Alegre and F. Ménard are thanked for their help in data processing. This work is a contribution to the cooperative agreement between the Instituto del Mar del Peru (IMARPE), the Institut de Recherche pour le Développement © 2014 The Fisheries Society of the British Isles, *Journal of Fish Biology* 2014, 84, 422–435
Supporting Information

Supporting Information may be found in the online version of this paper:

Table SI. Year, months, source, number of trawls, total number of stomachs (with prey contents) and length range (cm) of Engraulis ringens samples used to estimate the euphausiids fraction only.

Table SII. Results of Tukey-type multiple comparisons post hoc analyses of diatom contribution in Engraulis ringens diet by 2 cm long size class. In bold, significant differences ($P < 0.05$).

Table SIII. Results of Tukey-type multiple comparisons post hoc analyses of calanoids contribution in Engraulis ringens diet by 2 cm long size class. In bold, significant differences ($P < 0.05$).

Table SIV. Results of Tukey-type multiple comparisons post hoc analyses of euphausiids contribution in Engraulis ringens diet by 2 cm long size class. In bold, significant differences ($P < 0.05$).

Table SV. Results of Tukey-type multiple comparisons post hoc analyses of diatoms contribution in Engraulis ringens diet by $1^\circ$ of latitude. In bold, significant differences ($P < 0.05$).

Table SVI. Results of Tukey-type multiple comparisons post hoc analyses of calanoids contribution in Engraulis ringens diet by $1^\circ$ of latitude. In bold, significant differences ($P < 0.05$).

Table SVII. Results of Tukey-type multiple comparisons post hoc analyses of euphausiids contribution in Engraulis ringens diet by $1^\circ$ of latitude. In bold, significant differences ($P < 0.05$).

Table SVIII. Results of Tukey-type multiple comparisons post hoc analyses of diatoms contribution in Engraulis ringens diet according to the distance to the shelf break (negative inshore, positive offshore). In bold, significant differences ($P < 0.05$).

Table SIX. Results of Tukey-type multiple comparisons post hoc analyses of calanoids contribution in Engraulis ringens diet according to the distance to the shelf break (negative inshore, positive offshore). In bold, significant differences ($P < 0.05$).

Table SX. Results of Tukey-type multiple comparisons post hoc analyses of euphausiids contribution in Engraulis ringens diet according to the distance to the shelf break (negative inshore, positive offshore). In bold, significant differences ($P < 0.05$).

Table SXI. Results of Tukey-type multiple comparisons post hoc analyses of diatoms contribution in Engraulis ringens diet by diel period ($0700 \leq \text{day} < 1700$; $1700 \leq \text{dusk} < 1900$; $1900 \leq \text{night} < 0500$; $0500 \leq \text{dawn} < 0700$). In bold, significant differences ($P < 0.05$).

Table SXII. Results of Tukey-type multiple comparisons post hoc analyses of calanoids contribution in Engraulis ringens diet by diel period ($07:00 \leq \text{day} < 17:00$; $17:00 \leq \text{dusk} < 19:00$; $19:00 \leq \text{night} < 05:00$; $05:00 \leq \text{dawn} < 07:00$). In bold, significant differences ($P < 0.05$).

Table SXIII. Results of Tukey-type multiple comparisons post hoc analyses of euphausiids contribution in Engraulis ringens diet by diel period...
(07:00 ≤ day < 17:00; 17:00 ≤ dusk < 19:00; 19:00 ≤ night < 05:00; 05:00 ≤ dawn < 07:00). In bold, significant differences ($P < 0.05$).

References


