Long-term increase in crustacean zooplankton abundance in the southern Benguela upwelling region (1951–1996): bottom-up or top-down control?

Hans M. Verheye and Anthony J. Richardson

Since 1951, zooplankton samples have been collected on the shelf along the west coast of South Africa, where pelagic fish recruit each year. Retrospective analysis of collections made during peak recruitment in austral autumn showed a significant increase in the abundance of planktonic crustaceans by two orders of magnitude (from $3.74 \times 10^3$ ind. m$^{-2}$ in 1951 to $7.03 \times 10^5$ ind. m$^{-2}$ in 1996). This long-term increase was accompanied by a shift in the community size structure, which paralleled altered regimes of anchovy and sardine, two size-selective planktivores. The increase in crustacean zooplankton could be related to the observed long-term intensification of coastal upwelling in the region and a reduction in predation by declining stocks of pelagic fish over the past four decades.

Key words: Benguela Current, long-term trends, predation, upwelling, zooplankton.

Materials and methods

The zooplankton samples used for retrospective analysis were collected with 200-µm meshed nets on the shelf along the west coast of South Africa (since 1951).
Sample selection was restricted spatially to the St Helena Bay area and temporally to austral autumn (March–June), the centre and the peak period of recruitment of anchovy and sardine (Crawford et al., 1987). This region is the most productive on the west coast shelf (Mitchell-Innes and Walker, 1991) because of its position downstream of the Cape Columbine upwelling centre. Crustacean zooplankters, which contributed >97% of total zooplankton (Verheye et al., 1998), were identified and enumerated using standard analysis protocols. Species were classified into five size classes based on their total length: <0.9 mm (cyclopoids), 0.9–1 mm ( cladocerans and small calanoids), 1–2 mm (medium calanoids), 2–5 mm (large calanoids) and >5 mm ( euphausiids and amphipods). Counts (nos. m$^{-2}$) were log-transformed (log$_{10}$(x+1)) to reduce heteroscedasticity and improve normality. Prior testing for parallelism of regression slopes (StatSoft, 1996) of the abundance of the size classes against year showed the slopes to be significantly different ($p<0.001$; see Verheye et al., 1998). Multiple regressions were therefore computed for each size class, with year, month, distance offshore, surface temperature, and salinity as the independent variables. Non-significant ($p>0.05$) variables were removed in a backward stepwise process. Because of a 20-year hiatus between 1967 and 1987, separate regressions for the 1951–1967 and 1987–1996 periods were calculated, unless their respective slopes were not significantly different. Initial and final abundances were estimated for each model. A more detailed account of the data sources, sampling strategies, sample and statistical analyses, a list of species, and a critical evaluation of the data are given by Verheye et al. (1998).

### Results and discussion

Time series of the abundance of the crustacean size classes (Fig. 1), together with their respective slopes for the year effect, show that abundances (ind.m$^{-2}$) of several size categories increased significantly by two orders of magnitude (Fig. 1a, b, d):

<table>
<thead>
<tr>
<th>Size class</th>
<th>1951</th>
<th>1996</th>
</tr>
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<tbody>
<tr>
<td>&lt;0.9 mm</td>
<td>$0.91 \times 10^3$</td>
<td>$2.08 \times 10^5$</td>
</tr>
<tr>
<td>0.9–1 mm</td>
<td>$1.06 \times 10^3$</td>
<td>$2.90 \times 10^3$</td>
</tr>
<tr>
<td>2–5 mm</td>
<td>$0.63 \times 10^3$</td>
<td>$3.26 \times 10^4$</td>
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There was no consistent long-term trend in the abundance of the 1–2 mm size class, which tended to increase during 1951–1967 whilst declining from 1988 onwards, although neither slope was significant ($p>0.05$; Fig. 1c).

In the macrocrustacean size class (>5 mm), there was a difference in slopes between the periods 1951–1967 and
Crustacean zooplankton abundance in the southern Benguela upwelling region

1987–1996 (Fig. 1e). Nevertheless, their abundance increased significantly within each period:

<table>
<thead>
<tr>
<th>Size class</th>
<th>1951</th>
<th>1967</th>
<th>1988</th>
<th>1996</th>
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<tr>
<td>&gt;5 mm</td>
<td>0.05 \times 10^3</td>
<td>0.23 \times 10^3</td>
<td>0.16 \times 10^3</td>
<td>10.75 \times 10^3</td>
</tr>
</tbody>
</table>

With the exception of the distance offshore effect, which was positive for the 1–2 mm (1987–1996) and the >5 mm (1951–1967) size classes, year was the only independent variable examined that had a significant effect on the long-term variability in abundance.

Figure 2 shows a time series of the abundance of all size classes combined, together with a schematic representation of the bottom-up and top-down control mechanisms proposed. The abundance of planktonic crustaceans has increased significantly over the past 46 years, from 3.74 \times 10^3 in 1951 to 7.03 \times 10^5 ind.m^{-2} in 1996 (Fig. 2c). Moreover, the community size structure altered markedly through time: the proportion of <0.9 mm crustaceans increased whilst that of >1 mm crustaceans decreased (Fig. 3a), paralleling a regime shift from sardine to anchovy dominance (Fig. 3b).

The long-term increase in the overall abundance of crustacean zooplankton could be a consequence of several hydrographic and biological responses (Fig. 2d) to the long-term intensification of coastal upwelling in the Benguela Current region (Fig. 2e; see also Shannon et al., 1992). These include enhanced productivity (Mitchell-Innes and Walker, 1991, but see Figure 4 in Pitcher et al., 1992) within the semi-closed circulation system of the Cape Columbine–St Helena Bay region (Holden, 1985), combined with increased advective input of planktonic biota from the Cape Peninsula upwelling centre further south (Verheye, 1991; Verheye et al., 1991) and their retention within the study area (Verheye et al., 1992).

Alternatively, the increasing trend could also be caused by a long-term reduction in predation pressure by planktivorous pelagic fish, since declining pelagic catch data from 1960 onwards (Fig. 2b) suggest a decrease in stock size. This decline, in turn, may result from increased predation by apex predators such as snoek (Thyrsites atun) (Crawford et al., 1995; Fig. 2a) or the Cape fur seal (Arctocephalus pusillus pusillus) (see
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References


