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

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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 3.74×10^3 ind.m^{-2} in 1951 to 7.03×10^5 ind.m^{-2} in 1996). This long-term increase was accompanied by a shift in the community size structure, which parallelled 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.

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Introduction

Long-term trends in the abundance of zooplankton have been documented for a variety of aquatic systems worldwide. These are closely related to long-term changes in environmental parameters, with climatology often being the major driving force. In eastern boundary current systems such as the California Current (Roemmich and McGowan, 1995) and the Humboldt Current (Alheit and Bernal, 1993), zooplankton biomass has been observed to have decreased over the past few decades. These long-term declines in zooplankton may also be related to major changes in the abundance of small pelagic fishes (cf. Lluch-Belda *et al*., 1989).

As in other upwelling systems, the Benguela Current region on the west coast of southern Africa is characterized by coastal upwelling driven by equatorward wind stress (Parrish *et al.,* 1983). In the southern Benguela off South Africa, upwelling intensity has increased over the past four decades (Shannon *et al*., 1992), a phenomenon common to other upwelling-dominated systems (Bakun, 1990). In contrast to other upwelling regions, however, zooplankton abundance has significantly increased in that region during this period (Verheye *et al*., 1998).

Long-term time series of the abundance of crustacean zooplankton in different size categories are presented for the west coast of South Africa, where anchovy and sardine recruit to the pelagic fishery each year (Crawford *et al.*, 1987). These fish are size-selective planktivores, with sardine preferring smaller particles than anchovy (van der Lingen, 1994; Louw *et al*., 1998). Two possible causative mechanisms for the observed long-term trends in zooplankton abundance and community size structure, from both a bottom-up and top-down perspective, are explored. This article complements other contributions in this volume, where often only a bottom-up approach is considered to explain variability of zooplankton abundance.

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).

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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):

Size class	1951	1996
<0.9 mm	0.91×10^3	2.08×10^5
0.9–1 mm	1.06×10^3	2.90×10^5
2–5 mm	0.63×10^3	3.26×10^4

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

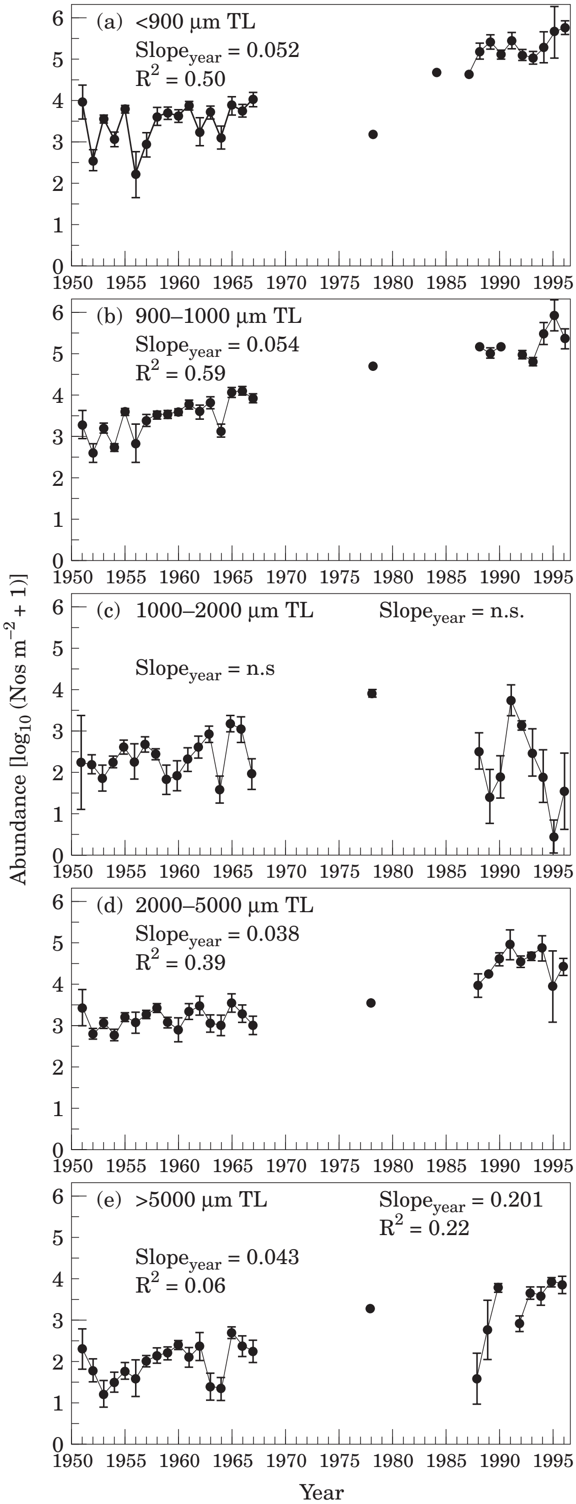
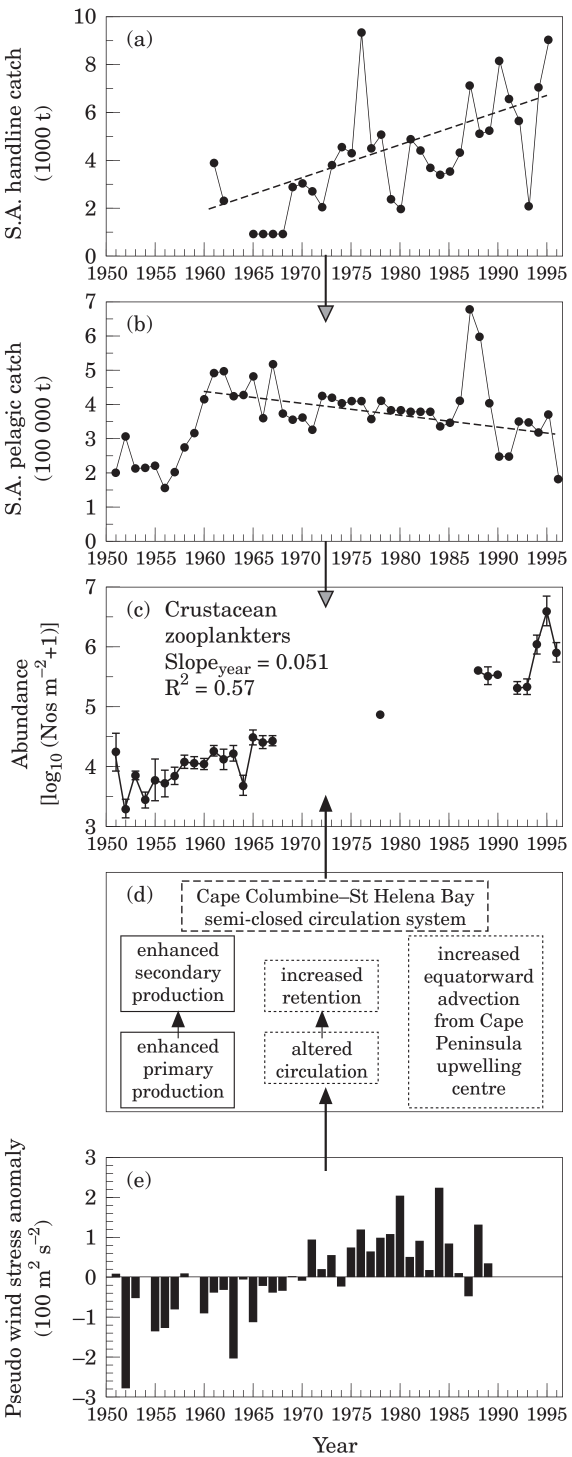


Figure 1. Time series of the annual (March–April) mean abundance [$\log_{10}$ (Nos $m^{-2}+1$)] of (a) <0.9 mm, (b) 0.9–1 mm, (c) 1–2 mm, (d) 2–5 mm, and (e) >5 mm crustacean zooplankton on the west coast of South Africa, 1951–1996. Error bars are ± 1 s.e.

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

Size class	1951	1967	1988	1996
>5 mm	0.05×10^3	0.23×10^3	0.16×10^3	10.75×10^3



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 3.74×10^3 in 1951 to 7.03×10^5 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

Figure 2. Schematic of possible causative mechanisms leading to the observed long-term increase in zooplankton in the southern Benguela region (open arrows: top-down control; solid arrows: bottom-up control): (a) time series of annual catch of snoek (*Thyrsites atun*) made by handline off South Africa, 1961–1995 (updated from Crawford *et al.*, 1995); (– – –) linear regression ($R^2_{adj.}$=0.39; p<0.001; n=33); (b) time series of annual landings of pelagic fish by the South African pelagic industry, 1951–1996 (updated from Schülein *et al.*, 1995); (– – –) post-1960 linear regression ($R^2_{adj.}$=0.47; p<0.001; n=35; outliers 1987 and 1988 excluded); (c) time series of the abundance [$\log_{10}$ (Nos m^{-2}+1)] of all crustacean zooplankters combined; error bars are ± 1 s.e. (regression equation: y=0.051x+0.996; n=204); (d) diagram of upwelling-related processes within the Cape Columbine–St Helena Bay semi-closed circulation system (cf. Verheye *et al.*, 1992); (e) time series of annual averaged anomalies of equatorward pseudo wind stress representing the southerly, upwelling-favourable component (redrawn from Shannon *et al.*, 1992).

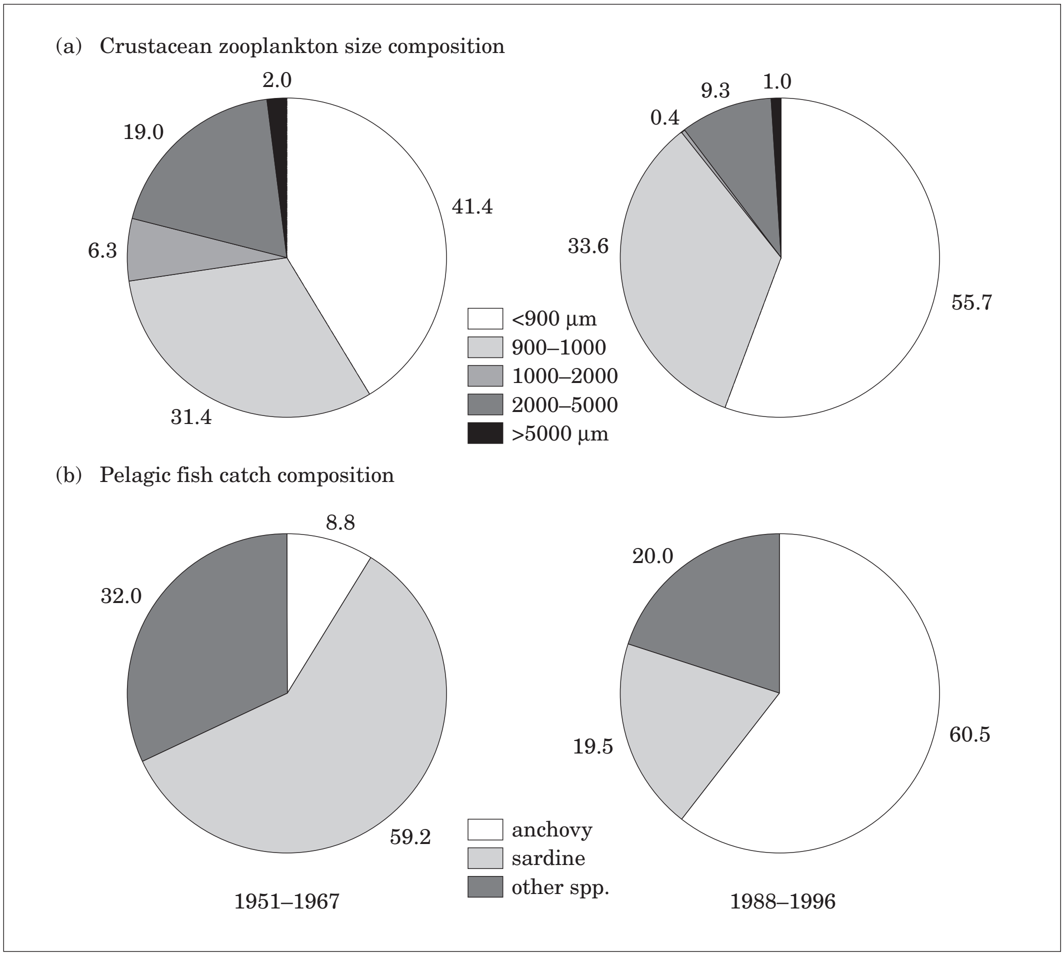


Figure 3. (a) Percentage composition of crustacean zooplankton size fractions averaged over the periods 1951–1967 and 1988–1996; (b) percentage composition of pelagic fish catches, averaged over the same periods; "other spp." include predominantly horse mackerel (*Trachurus trachurus capensis*), round herring (*Etrumeus whiteheadi*), chub mackerel (*Scomber japonicus*), and myctophids.

Butterworth *et al.*, 1995), the population of which has grown rapidly in recent decades as it recovers from overexploitation.

Both bottom-up and top-down mechanisms could be simultaneously responsible for the long-term increase in zooplankton in the southern Benguela, although their relative importance cannot be assessed. That predation could have caused, or contributed to, this long-term trend is in contrast to other studies (e.g. Aebischer *et al.*, 1990) where climate alone has been suggested as the causative mechanism for long-term changes at various trophic levels.

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