

Comparative Trophodynamics of *Sardine Sardinops sagax* and Anchovy *Engraulis capensis* in the Southern Benguela

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INTRODUCTION

The Benguela Current system extends along the southwest coast of Africa, from its northern boundary at approximately 15°S, to its southern boundary at Cape Agulhas (35°S) (SHANNON 1985). A perennial upwelling cell at Luderitz, Namibia, (25-27°S) divides the Benguela system into northern and southern regions (AGENBAG and SHANNON 1988), and is thought to be an environmental barrier which limits the interchange of pelagic fish populations (AGENBAG 1980). The Benguela system is characterised by wind-driven coastal upwelling, and like other upwelling systems, supports several large fisheries. The pelagic fishery, which is dominated by sardine *Sardinops sagax* and anchovy *Engraulis capensis* is centred off Walvis Bay in Namibia, and off the southwest Cape in South Africa. Catches have fluctuated widely, and apparently independently, in the northern and southern regions. In the southern Benguela, sardine catches peaked at 400,000 tons in 1962, and are currently about 100,000 tons per annum, of which 60,000 tons is directed catch and 40,000 tons is bycatch (ARMSTRONG and THOMAS 1989; Chief Directorate Sea Fisheries 1995). Since 1966, however, anchovy has been the dominant pelagic species in the southern Benguela (CRAWFORD *et al.*, 1987), with landings ranging from 150,000 to 600,000 tons annually (HUTCHINGS 1992).

Sardine/anchovy species pairs are found in several other eastern boundary current systems, including the California, Humboldt and Canary currents, and also in the coastal waters of Japan (CRAWFORD 1987). Like the Benguela, these systems have been extensively fished, and have shown large-scale fluctuations in sardine and anchovy populations, with sardine often abundant when

anchovy are scarce and vice versa (CRAWFORD 1987). This occurrence of worldwide, longterm fluctuations in sardine and anchovy populations, termed the "regime problem" (LLUCH-BELDA *et al.*, 1989), is currently receiving considerable attention (LLUCH-BELDA *et al.*, 1992a). Evidence from the sedimentary record of anaerobic basins (SOUTAR and ISAACS 1969) indicates that such fluctuations occurred in the past, long before the advent of fishing, and implies that they were attributable to causes other than fishing (LASKER 1985).

The causes of such species replacements, which occur over relatively short time periods but persist for decades, are not well understood. Interspecific competition for food and/or space was originally invoked as a causal mechanism of regime shifts (DAAN 1980; SCUD 1982; LASKER and MACCALL 1983; LASKER 1985), whilst later studies implicated interspecific predation on eggs and early larvae (ALHEIT 1987; VALDES SZEINFELD and COCHRANE 1992). In contrast, KAWASAKI (1992) suggested that fluctuations in temperate pelagic fish communities were principally determined by changes in the abundance of sardine, which, as a phytoplanktivore, is one of the closest species to first-level production, and is therefore the most strongly influenced by climatic changes. Other studies have suggested that the mechanisms driving species replacements may be associated with structural changes in the ecosystem, and with long-term environmental variations of basin-wide to global scale (LLUCH-BELDA *et al.*, 1989; Scientific Committee of Oceanic Research 1994), termed "global teleconnections" (Food and Agriculture Organization 1995). For example, LLUCH-BELDA *et al.*,

(1992b) revealed a strong similarity between the abundance and distribution of sardine and long term changes in sea-surface temperature in both the California and the Humboldt current systems. Global teleconnections notwithstanding, a major question concerning regime shifts is how to link global variability to the biological populations involved (Scientific Committee of Oceanic Research, 1994). Whatever the mechanisms governing these processes, there is accumulating evidence that in all four regions where sardine is heavily fished (i.e. the Japanese, Californian, Humboldt and Benguela systems), recent changes in relative abundance of sardine and anchovy were initiated during the 1980s (LLUCH-BELDA *et al.*, 1992a). During the 1990s, sardine populations declined rapidly off Japan and Peru, but increased off California and in the Benguela system (Scientific Committee of Oceanic Research, 1994). In the southern Benguela, there is evidence that a regime shift may be currently underway, from an anchovy-dominated to a sardine dominated system (Sea Fisheries Research Institute unpublished data).

This paper compares the dynamics of adult sardine and anchovy from the southern Benguela, with the objective of describing trophic interactions between this species pair, and possibly elucidating feeding-related mechanisms that could be linked to regime changes. The trophodynamics of anchovy have been extensively analyzed (JAMES 1988a; JAMES *et al.*, 1989a; JAMES *et al.*, 1989b), but only partially examined for sardine (VAN DER LINGEN 1994; VAN DER LINGEN 1995). Where sufficient data for both species exist, the trophodynamic aspects are compared and contrasted.

FEEDING BEHAVIOUR

Both sardine and anchovy are very flexible in their feeding behaviour and possess two feeding modes, namely filter and particulate-feeding. Filter-feeding fish swim in a tight school with their mouths opened wide and their operculae markedly flared, and collect food particles on their gill rakers. Particulate-feeding fish do not school, but independently align themselves

toward specific food particles, which they then engulf. Particle size is the prime determinant of feeding mode choice, and although sardine and anchovy have different threshold sizes, both species filter-feed on small particles and particulate feed on large particles.

Filter-feeding is the principal feeding mode of sardine. Food particles of less than 1.2 mm elicit a filtering response, whilst larger particles elicit particulate-feeding at low concentrations but filter-feeding at high concentrations (VAN DER LINGEN 1994). The rate at which food particles are removed from the water (called the clearance rate) during filtering is independent of particle size over the size range 0.4 - 1.2 mm (maximum dimension), with a mean value of $11.8 + 4.9 \text{ l fish}^{-1} \text{ minute}^{-1}$. This value is 93% of the calculated maximum clearance rate for filtering fish, implying that sardine are highly efficient at filter-feeding over this size range. Sardine is less efficient at retaining particles of smaller size, but are able to entrap particles down to 0.02 mm in size. They are therefore able to directly feed on netphytoplankton. Clearance rates during particulate-feeding are greater than those during filtering, and increase with increasing particle size to a predicted maximum value of $46.5 \text{ litres fish}^{-1} \text{ minute}^{-1}$.

Particulate-feeding is the primary feeding mode for anchovy, which switch from filter to particulate-feeding at a threshold prey size of 0.7 mm (JAMES and FINDLAY 1989). The minimum particle size that can be entrapped during filtering is 0.20 - 0.25 mm. Clearance rates during particulate-feeding are greater than those during filtering, and reach a maximum saturation value of $17.0 \text{ litres fish}^{-1} \text{ minute}^{-1}$. Anchovy are highly size-selective, selecting for the largest particle available.

A comparison of predictive equations of clearance rate as a function of particle size for both species demonstrates that sardine show substantially higher clearance rates than anchovy, across the entire prey size spectrum (VAN DER LINGEN 1994). However, when clearance rates are standardized and expressed as a function of fish weight (i.e. $\text{g}^{-1} \text{ minute}^{-1}$), sardine are only more efficient at removing particles of less than 0.6mm in size, anchovy having distinctly higher weight specific

clearance rates on particles larger than this size. Sardine therefore are more efficient removers of small particles, whilst anchovy remove large particles more effectively.

FEEDING COSTS AND METABOLISM

The energetic costs of feeding, for both sardine and anchovy, have been determined through the measurement of respiration rates during non-feeding, filter-feeding and particulate feeding. For both species, respiration rate increases with swimming speed for all activity states, although the shape of the functional relation differs between species, being linear for sardine (VAN DER LINGEN 1995) but log-linear for anchovy (JAMES and PROBYN 1989). The relative energetic costs of each feeding mode were determined from the slope of the respiration rate/swimming speed regression derived for each species displaying both feeding modes, with higher slope values indicating higher relative energetic cost.

At any given swimming speed, filter-feeding by adult sardine is energetically cheaper than particulate-feeding (VAN DER LINGEN 1995). This is in contrast to anchovy, where particulate-feeding is the energetically cheapest feeding mode (JAMES and PROBYN 1989). JAMES and PROBYN (1989) argued that the change in body shape and increased drag associated with flared operculae during filter-feeding was responsible for the increased metabolic costs. Following JAMES and PROBYN's (1989) line of reasoning, it would intuitively be expected that this would also apply to sardine, since the act of filtering also results in marked changes in body shape. However, viscous force, which is proportional to fish surface area (WEBB 1975) and results in drag, is only one of the forces acting upon a fish. Inertial force, which is proportional to fish mass, also acts upon bodies moving in fluids (WEBB 1975).

The relative importance of inertial and viscous forces is expressed in the dimensionless Reynolds Number (R), which is a function of organism size, velocity, fluid density and kinematic viscosity (VIDELER 1993). Viscous forces are dominant for small organisms, whereas inertial forces are dominant for larger organisms (WEBB 1975 VIDELER 1993). The relative importance of

viscous forces is therefore likely to be higher for anchovy, since anchovy are smaller than sardine. Furthermore, at any given swimming speed anchovy will have a lower R although inertial forces will dominate for both species. Estimates of R range from 4.2×10^4 to 1.1×10^5 for sardine, and 1.7×10^4 to 4.2×10^4 for anchovy, swimming from 20 to 50 $\text{cm}\cdot\text{s}^{-1}$ at 15°C (VAN DER LINGEN 1995). This difference between sardine and anchovy may be the reason for the observed differences in feeding-mode metabolic costs. Thus capturing prey by particulate-feeding is relatively more expensive for the larger pilchard, whereas the increased drag associated with filter-feeding is relatively more expensive for the smaller anchovy.

The experimental procedure used in determining the energetic costs of feeding also allowed estimation of the respiratory quotient (RQ) for each species. Respiratory quotients indicate the type of physiological fuel involved in metabolism, and ranges from 0.7 for the catabolism of fats, through 0.9 for protein, to 1.0 for carbohydrates (BRETT and GROVES 1979). A mean RQ value of 0.96 was determined for sardine (VAN DER LINGEN 1995), suggesting that metabolism is based on the breakdown of both protein and carbohydrates. JAMES and PROBYN (1989) estimated an RQ of 0.92 for anchovy, and suggested that protein was the metabolic fuel for this species. The higher RQ value for sardine suggests a greater carbohydrate utilization by this species compared to anchovy.

A higher capacity to utilize carbohydrates is characteristic of herbivorous species (BRETT and GROVES 1979), and implies that phytoplankton is a more important dietary component for sardine than anchovy, although both species consume phytoplankton (JAMES 1988b).

DIET AND FEEDING ECOLOGY

Field-based research examining the feeding of sardine in the southern Benguela indicated that they were primarily filter feeders showing an apparent "preference" for phytoplankton, and having a mean ratio of phytoplankton to zooplankton in their stomachs of 2:1 by volume (DAVIES 1957). KING and MACLEOD (1976), working in Namibia, suggested that juvenile sardine were zooplanktophagous, feeding predominantly

on calanoid copepods, but switched to phytoplanktons at approximately 100 mm standard length. Adult sardine were regarded as essentially non-selective filter-feeders; the change from selective zooplanktivory to nonselective phytoplanktivory being attributed to a reduction in gill-raker gap and increased ability to retain small particles (KING and MACLEOD 1976). However, the inclusion of intestinal contents in the analysis and the use of frequency-of-occurrence data to illustrate food item importance, as employed by KING and MACLEOD (1976), was shown to overestimate the importance of digestion-resistant and/or small food particles such as diatoms. These processing techniques have been criticized as inadequate (HYSLOP 1980; JAMES 1987).

Preliminary studies on the diet of sardine from the southern Benguela (VAN DER LINGEN in prep) showed that sardine ingest both phytoplankton and zooplankton, and whilst phytoplankton appear to be more important volumetrically, the relative dominance of each fraction appears to be influenced by location. However, further data analysis is required. In samples analyzed to date, the frequency distribution of ingested zooplankton closely matched that of ambient prey size distribution, indicating non-selective feeding. Substantial quantities of microzooplankton, including copepod eggs, nauplii and copepodites, as well as adults of small copepod species, are also frequently found in sardine stomachs (VAN DER LINGEN in prep.).

Sardine do not appear to be obligate vertical migrators, but tend to form small, scattered schools by night and dense schools by day (HAMPTON *et al.*, 1979; THOMAS and SCHULEIN 1988), whilst generally remaining in the top 20 - 30m of the water column. However, they have on occasion been observed to undertake significant diet vertical migration (VAN DER LINGEN in prep.). No obvious feeding periodicity cycle has been observed for this species.

KING and MACLEOD (1976), described the diet and feeding ecology of anchovy in the northern Benguela, concluded that adult anchovy were phytoplanktivorous, with diatoms comprising the bulk of their diet. Fish switched from selective particulate-feeding on zooplankton when juvenile

to non-selective filter-feeding when adult. However, the criticisms of their methodology discussed above also apply here. KING and MACLEOD's (1976) findings were refuted by JAMES (1987), who demonstrated that mesozooplankton, principally calanoid copepods and euphausiids, were the dominant dietary component of adult anchovy in the southern Benguela. JAMES (1987) further showed that adult anchovy fed predominantly through particulate-feeding, and were distinctly size selective.

In addition to these findings, JAMES (1987) observed that anchovy displayed a marked cycle in feeding behaviour, with peak feeding occurring at night. This diel feeding cycle was associated with vertical migration (THOMAS and SCHULEIN 1988), with high feeding activity at night coinciding with shoal dispersal in the surface waters, and low feeding activity during the day coinciding with shoal aggregation and descent into deeper water.

Recent studies have examined the shoaling characteristics of both sardine and anchovy in the southern Benguela, through the use of acoustic echo-integration techniques. These have revealed significant diel changes in packing density of anchovy, with schools having a higher packing density during the day than during the night. No such difference in packing density was observed for sardine (Sea Fisheries Research Institute unpublished data). Such studies further corroborate the hypothesis that anchovy are predominantly particulate-feeders, whereas sardine primarily filter-feed, since a reduction in school density by particulate-feeding anchovy at night reduces the overlap of individual visual fields (EGGERS 1976) and hence reduced intraspecific competition. This reduction in school density is unnecessary for the filter-feeding sardine.

DISCUSSION

The experiments reported here demonstrate that *Sardinops sagax* is primarily a filter-feeder, which exhibits a high weight-standardised clearance rate on small food particles. Moreover, filter-feeding is the energetically-cheapest feeding mode of this species. In contrast, *Engraulis capensis* is predominantly a particulate-feeder, with low weight standardised clearance rates on small particles

but elevated rates on large particles. Particulate-feeding is the energetically cheapest feeding mode for this species.

That sardine are primarily filter-feeders, and anchovy primarily particulate-feeders, is confirmed by studies of their diet and *in situ* feeding behaviour: the major dietary component of sardine in the southern Benguela are microzooplankton and phytoplankton, collected through filter-feeding whereas the major dietary components of anchovy are mesozooplankton, which are caught by particulate-feeding.

The difference in weight-standardised clearance rates of sardine and anchovy feeding on different-sized food particles, coupled with the difference in relative energetic costs of their predominant feeding modes, implies that the size spectrum of the planktonic food environment will have important ramifications for the feeding success of each species. Food environments dominated by small particles will favour sardine over anchovy, since sardine are more efficient removers of small particles, and can collect such food particles through employing relatively cheap filter-feeding. Hence sardine will have a higher net energetic gain in small particle-dominated environments than anchovy.

Anchovy, on the other hand, are inefficient removers of small particles, and filter-feeding is the energetically most expensive feeding mode for this species. Food environments comprising mainly large particles will favour anchovy over sardine, due to the anchovy's higher efficiency at removing large particles through relatively cheap particulate-feeding.

Sardine, in addition to being less efficient removers of large particles than anchovy, have to acquire such food through expensive particulate-feeding, unless such particles are present in sufficiently high concentrations to elicit filter-feeding. Anchovy will therefore show a higher net energetic gain in large particle-dominated environments than anchovy.

Complex spatial and temporal variations in prey size-range and concentration typify pelagic food environments (JAMES 1988b).

It has recently been demonstrated in the southern Benguela that, size structure and biomass of phy-

toplankton populations are closely related to physico-chemical conditions resulting from physical forcing mechanism (MITCHELL-INNES and PITCHER 1992). Under intermittent mixing conditions, such as those that occur during upwelling, water temperatures vary between 12 and 15°C, and sporadic nutrient enrichment of the euphotic zone occurs. This promotes the development of phytoplankton populations of high biomass, dominated by large, chain-forming diatoms. Conversely, under very stable conditions, warm temperatures (>15°C) and nutrient depletion of the upper layers limit diatom growth, enabling small nanoflagellate populations to predominate (MITCHELL-INNES and PITCHER 1992).

In turn, zooplankton community structure has been shown to be affected by phytoplankton community and size structure (VERHEYE *et al.*, 1992). Large copepods (e.g. *Calanoides* and *Rhincalanus*) display enhanced growth rates under diatom dominated conditions, whereas small species (e.g. *Oithona*) show elevated growth rate when small cells are dominant (VERHEYE *et al.*, 1993). Different physical scenarios can therefore lead to food environments being dominated by either small or large particles. As a consequence of their different trophodynamics, long-term fluctuations in sardine and anchovy stocks in the southern Benguela may co-vary with structural changes in phytoplankton and zooplankton assemblages, resulting from alterations in the prevailing physical environment (VERHEYE *et al.*, 1993).

The evidence presented here supports the hypothesis that regime shifts between sardine and anchovy are associated with structural changes in the ecosystem, leading to environments which favour one species over the other. Trophodynamics will play an important role in determining the success of each species under particular environmental conditions, although these differences alone are unlikely to account for regime shifts. Rather, trophodynamics should be considered in conjunction with spawning success, egg and larval transport, larval and juvenile feeding success and other factors affecting recruitment, and expansion and contraction of species ranges under different

conditions. The trophodynamic differences also imply resource partitioning between adults of the two species, in contrast to previous suggestions of competition for food (LASKER and MACCALL 1983; LASKER 1985).

REFERENCES

- Agenbag, J. J. (1980). General distribution of pelagic fish off South West Africa as deduced from aerial fish spotting (1971-1974 and 1977) as influenced by hydrology. *Fish. Bull. S. Afr.* 13: 55-67.
- Agenbag, J. J. and L.V. Shannon, (1988). A suggested physical explanation for the existence of a biological boundary at 24°30' S in the Benguela System *S. Afr. J. mar. Sci.* : 119-132 .
- Alheit, J. (1987). Egg cannibalism versus egg predation: their significance in anchovies. In: Payne, A.I.L., Gulland, J.A. and Brink, K.H. (Eds.) *The Benguela and Comparable Ecosystems. S. Afr. J. mar. Sci.* 5: 467-470.
- Armstrong, M.J. and R.M. Thomas, (1989). Clupeoids. In: Payne, A.I.L. and Crawford, R.J.M. (eds.) *Oceans of Life off Southern Africa*. Vlaeberg, Cape Town, P. 105-121.
- Brett, J.R. and T.D.D. Groves, (1979). Physiological energetics. In: Hoar, W.S. , Randall, D.J. and Brett, J.R. (Eds.) *Fish Physiology Vol.VIII. Energetics and Growth*. Academic Press, New York, p. 279-352.
- Chief Directorate Sea Fisheries (1995). *South African Commercial Fisheries Review 1993*. 3. Department of Environmental Affairs and Tourism: South Africa.
- Crawford, R. J. M. (1987). Food and population variability in five regions supporting large stocks of anchovy, sardine and horse mackerel. In: Payne, A.I.L., Gulland, J.A. and Brink, K.H. (Eds.) *The Benguela and Comparable Ecosystems. S. Afr. J. mar. Sci.* 5: 735-757.
- Crawford, R.J.M., L.V. Shannon, and D.E. Pollock, (1987). The Benguela ecosystem. 4. The major fish and invertebrate resources. In: Barnes, M. (Ed.) *Oceanography and Marine Biology, An Annual Review 25* . Aberdeen; University Press: 353-505.
- Daan, N. (1980). A review of replacement of depleted stocks by other species and the mechanisms underlying such replacement. *Rapp. P. -v. Reun. Cons. int. Explor. Mer.* 177: 405-421.
- Davies, D.H. (1957). The South African pilchard (*Sardinops ocellata*). Preliminary report on feeding off the west coast, 1953-56. *Investl. Rep. Div. Fish. S. Afr.* 30: 1 - 40.
- Eggers, D.M. (1976). Theoretical effect of schooling by planktivorous fish predators on rate of prey consumption. *J. Fish. Res. Bd. Can.* 33: 1964-171.
- Food and Agriculture Organization. (1995). *The state of world fisheries and aquaculture*. Food and Agriculture Organization of the United Nations, Rome. 57 pp.
- Hampton, I., J.J. Agenbag, and D.L. Cram, (1979). Feasibility of assessing the size of the South West African pilchard stock by combined aerial and acoustic measurements. *Fish. Bull. S. Afr.* 11: 10-22.
- Hutchings, L. (1992). Fish harvesting in a variable, productive environment - searching for rules or searching for exceptions? In: Payne, A.I.L., Mann, K.H. and Hilborn, R. (Eds.) *Benguela Trophic Functioning. S. Afr. J. Mar. Sci.* 12: 297-318.
- Hyslop, E.J. (1980). Stomach contents analysis - a review of methods and their application. *J. Fish Biol.* 17(4): 411-429.
- James, A.G. (1987). Feeding ecology, diet and field-based studies on feeding selectivity of the Cape anchovy *Engraulis capensis* Gilchrist. In: Payne, A.I.L. Gulland, J.A. and Brink, K.H. (eds.) *The Benguela and Comparable Ecosystems. S. Afr. J. mar. Sci.* 5: 597-611.
- James, A.G. (1988a). The feeding ecology of and carbon and nitrogen budgets for *Engraulis capensis* in the southern Benguela ecosystem. Ph.D. thesis, University of Cape Town, 231 p.
- James, A.G. (1988b). Are clupeoid microphagists, herbivorous or omnivorous? A review of the diets of some commercially important clupeids. *S. Afr. J. mar. Sci.* 7: 161-177.
- James, A.G. and K.P. Findlay, (1989). Effect of particle size and concentration on feeding behaviour, selectivity and rates of food ingestion by the Cape anchovy *Engraulis capensis*. *Mar. Ecol. Prog. Ser.* 50: 275-294.

- James, A.G. and R. Probyn, (1989). The relationship between respiration rate, swimming speed and feeding behaviour in Cape anchovy *Engraulis capensis*. *Gilchrist. J. Exp. Mar. Biol. Ecol.* 131: 81-100.
- James, A.G., T. Probyn, and L.J. Seiderer, (1989a). Nitrogen excretion and absorption efficiencies of the Cape anchovy *Engraulis capensis* Gilchrist fed upon a variety of plankton diets. *J. Exp. Mar. Biol. Ecol.* 131: 101-124.
- James, A.G., T. Probyn, and L. Hutchings, (1989b). Laboratory-derived carbon and nitrogen budgets for the omnivorous planktivore *Engraulis capensis*. *Gilchrist. J. Exp. Mar. Biol. Ecol.* 131: 124-145.
- Kawasaki, T. (1992). Mechanisms governing fluctuations in pelagic fish populations. In: Payne, A.I.L., Mann, K.H. and Hilborn, R. (eds.) *Benguela Trophic Functioning. S. Afr. J. Mar. Sci.* 12: 873-879.
- King, D.P.F. and P.R. Macleod, (1976). Comparison of the food and filtering mechanism of pilchard *Sardinops ocellata* and anchovy *Engraulis capensis* off South West Africa, 1971-1972. *Investl. Rep. Sea Fish. Brch S. Afr.* 111: 1-29.
- Lasker, R. (1985). What limits clupeoid production? *Can. J. Fish. Aquat. Sci.* 421(Suppl.1): 31-38.
- Lasker, R. and A. MacCall, (1982). New ideas on the fluctuations of the clupeoid stocks off California. *Proc. Joint Oceanogr. Assembly 1982 - General Symposia, Can. Nat. Comm./Scientific Comm. Ocean. Res., Ottawa, Ont., p. 110-120.*
- Lluch Belda, D., R.J.M. Crawford, T. Kawasaki, A.D. MacCall, R.H. Parrish, R.A. Schwarzlose, and P.E. Smith, (1989). World-wide fluctuations of sardine and anchovy stocks: the regime problem. *S.Afr. J. Mar. Sci.* 8: 195-205.
- Lluch-Belda, D., R.A. Schwarzlose, R. Serra, R. Parrish, T. Kawasaki, D. Hedgecok, and R.J.M. Crawford, (1992a). Sardine and anchovy regime fluctuations of abundance in four regions of the world oceans: a workshop report. *Fish. Oceanogr.* 1: 339-347.
- Lluch-Belda, D., D.B. Lluch-Cota, S. Hernandez-Vazques, and C.A. Salinas-Zavala, (1992b). Sardine population expansion in eastern boundary systems of the Pacific Ocean as related to sea surface temperature. In: Payne, A.I.L., Mann, K.H. and Hilborn, R. (eds.) *Benguela Trophic Functioning. S. Afr. J. Mar. Sci.* 12: 147-155.
- Mitchell-Innes, B.A. and G.C. Pitcher, (1992). Hydrographic parameters as indicators of the suitability of phytoplankton populations as food for herbivorous copepods. In: Payne, A.I.L., Mann, K.H. and Hilborn, R. (eds.) *Benguela Trophic Functioning. S. Afr. J. Mar. Sci.* 12: 355-365.
- Scientific Committee of Oceanic Research (1994). Worldwide large-scale fluctuations of sardine and anchovy populations. Report of the First Meeting of Working Group 98, La Paz, Baja California, Mexico, 13-17 June 1994.
- Scud, B.E. (1982). Dominance in fishes: the relation between environment and abundance. *Science* 216: 144-149.
- Shannon, L.V. (1985). The Benguela Ecosystem. 1. Evolution of the Benguela, physical features and processes, In: Barnes, M. (eds.) *Oceanography and Marine Biology. An Annual Review* 23: 105-182.
- Soutar, A. and J.D. Isaacs, (1969). History of fish populations inferred from fish scales in anaerobic sediments off California, Calif. *Coop. Oceanic Fish. Invest. Rep.* 13: 63-70.
- Thomas, R.M. and F.H. Schuelein, (1988). The schooling behaviour of pelagic fish and the distribution of seals and gannets off Namibia as deduced from routine fishing reports, 1982-1985. *S.Afr. J. Mar. Sci.* 7: 179-191.
- Valdes Szeinfeld, E.S. and K.L. Cochrane, (1992). The potential effects of cannibalism and intraguild predation on anchovy recruitment and clupeoid fluctuations. In: Payne, A.I.L., Mann, K.H. and Hilborn, R. (Eds.) *Benguela Trophic Functioning. S. Afr. J. Mar. Sci.* 12: 695-702.
- van der Lingen, C.D. (1994). Effect of particle size and concentration on the feeding behaviour of adult pilchard *Sardinops sagax*. *Mar. Ecol. Prog. Ser.* 109: 1-13.

- van der Lingen, C.D. (1995). Respiration rate of adult pilchard *Sardinops sagax* in relation to temperature, voluntary swimming speed and feeding behaviour. *Mar. Ecol. Progr. Ser.* In press.
- van der Lingen, C.D. (in prep). Diet and daily ration of pilchard *Sardinops sagax* in the southern Benguela.
- Verheye, H.M., L. Hutchings, J.A. Huggett, and S.J. Painting, (1992). Mesozooplankton dynamics in the Benguela ecosystem, with emphasis on the herbivorous copepods. In: Payne, A.I.L., Mann, K.H. and Hilborn, R. (Eds.) Benguela Trophic Function. *S. Afr. J. Mar. Sci.* 12: 561-584.
- Verheye, H.M., B.A. Mitchell-Innes, and C.D. van der Lingen, (1993). Size-based relationships in the pelagic food web of the southern Benguela. Programme and Abstracts, 8th Southern African Marine Science Symposium, 17-22 October 1993, Club Mykonos, Saldanha Bay.
- Videler, J.J. (1993). Fish Swimming. Chapman and Hall, London 260p.
- Webb, P.W. (1975). Hydrodynamics and energetics of fish propulsion. *Bull. Fish. Res. Bd. Can.* 190: 159p.