S. Afr. J. mar. Sci. 18: 107–112
1997

ANCHOVY BIOMASS IS LINKED TO ANNUAL POTENTIAL NEW PRODUCTION IN THE SOUTHERN BENGUELA: SUPPORT FOR THE "OPTIMAL ENVIRONMENTAL WINDOW" HYPOTHESIS

*H. N. WALDRON**, *G. B. BRUNDRIT** and *T. A. PROBYN*†

The hypothesis that physical forcing is related to tertiary production was tested by relating regional estimates of annual potential new production to certain pelagic fishery variables. The results show strong evidence of a dome-shaped relationship between annual potential new production (x-axis) and anchovy spawner biomass (y-axis), providing further confirmation that both a paucity and surfeit of upwelling is detrimental to the fishery. Fish biomass was maximized by a median range of upwelling, which formed an "Optimal Environmental Window" either side of the dome apex. The relationship was described by a Gaussian Area curve:

$$y = 1.90\ e^{[-0.5((x-5.72)/0.43)^2]} \cdot\ (r^2 = 0.90) \quad .$$

A similar, but less marked, dome-shaped relationship was found with respect to anchovy recruitment biomass. It is shown that the period of physical forcing most likely to impact on anchovy recruitment on the west coast of South Africa is negatively correlated with recruitment biomass.

The work of Iverson (1990) supported the hypothesis that carnivorous fish (and squid) production is controlled by the quantity of new nitrogen (NO_3-N) incorporated annually into phytoplankton biomass (annual new production) and transferred through marine foodwebs. This hypothesis is tested here in the context of the southern Benguela upwelling system, using estimates of annual potential new production provided in Waldron *et al.* (1997) and information relating to the pelagic fishery. Potential new production is a physical index of upwelling. It is the amount of NO_3-N made available to phytoplankton via upwelling dynamics as opposed to the amount of NO_3-N actually incorporated into their biomass.

Anchovy *Engraulis capensis* is a major pelagic resource in South Africa. The southern stock is found and harvested on the West Coast (southern Benguela) and adults spawn over the Agulhas Bank. The distribution and movements of anchovy at various life stages have been well established (Crawford 1980, 1981, Shelton and Hutchings 1982, Armstrong *et al.* 1985, Shelton 1986, Hampton 1987). A summary of those findings describes a fish population which spawns during spring and summer, predominantly on the western Agulhas Bank. Ichthyoplankton is entrained west and north into the southern Benguela and is recruited into the adult population during autumn and winter. The adults then migrate south, inshore along the West Coast, reaching the Agulhas Bank towards the end of their first year of life. James (1987) found that the major component of the anchovy diet consisted of mesozooplankton, especially calanoid copepods and euphausiids. This finding was contrary to the prevailing view that they were non-selective, filter-feeding omnivores, deriving the bulk of their nutrition from diatoms. Such a finding extends the trophic distance between new production and fish, which necessitated careful consideration of appropriate timescales when attempting to relate the two variables.

A simple model describing the link between new production and fish would depict a positive, linear relationship between upwelling frequency and intensity, and certain variables relating to the fishery (*inter alia* spawner and recruitment biomass). The greater the upwelling, the more NO_3-N is introduced into the euphotic zone, which would benefit the fishery via the phytoplankton-zooplankton food chain. This simplistic approach has been modified following the work of Cury and Roy (1989) and Roy *et al.* (1992), who described an "Optimal Environmental Window" (OEW) hypothesis to accommodate the apparently contradictory evidence of both negative and positive relationships between recruitment and upwelling indices. Their hypothesis assumed a dome-shaped curve between recruitment and upwelling, which considered both weak and strong upwelling intensities to be detrimental to the fishery. A zone either side of the dome apex was defined as the OEW. Cury and Roy (1989) and Roy *et al.* (1992) used wind speed as a proxy for upwelling, finding the OEW to be between 5 and 6 $m \cdot s^{-1}$. Roy *et al.* (1992) reported that Mendelssohn (1989) obtained similar results for the Peruvian anchoveta *Engraulis ringens* and Ware and Thompson (1991) supported the existence of an

* Department of Oceanography, University of Cape Town, Private Bag, Rondebosch 7701, South Africa. E-mail: waldron@physci.uct.ac.za
† Formerly University of Cape Town; now Sea Fisheries Research Institute, Private Bag X2, Rogge Bay 8012, Cape Town, South Africa. E-mail: tprobyn@sfri.wcape.gov.za

Manuscript received: June 1996

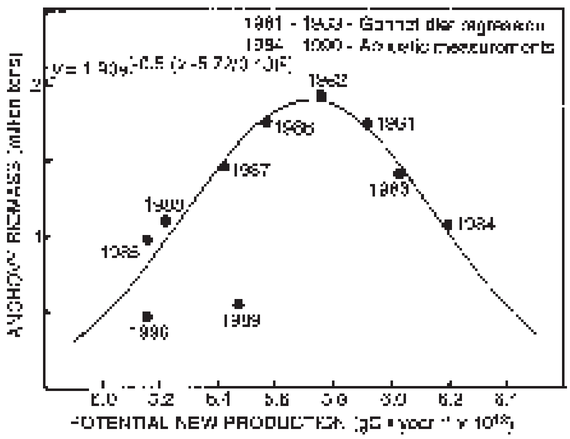

Fig. 1: Relationship between annual potential new production and anchovy spawner biomass (derived from gannet diet regressions and acoustic measurements), 1981–1990. The equation is described by a Gaussian Area curve

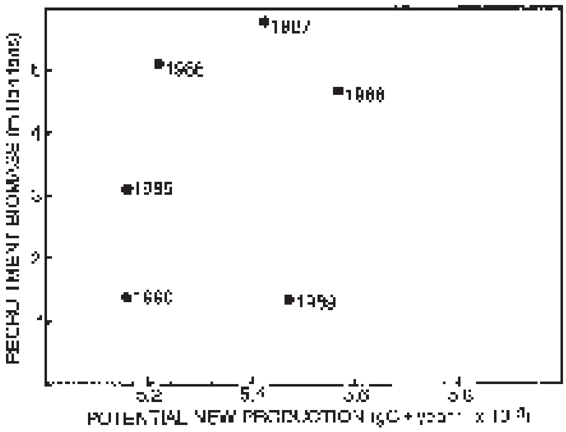

Fig. 2: Relationship between annual potential new production and survey estimates of anchovy recruitment biomass (measured acoustically at the end of the potential new production period, i.e. in May of each year), 1985–1990

OEW for the Pacific sardine *Sardinops sagax*, but at a faster wind speed. Orbi *et al.* (1991) showed that, for the Moroccan sardine *Sardina pilchardus,* the relationship between catch per unit effort (*cpue*) and the upwelling indices of the previous two years were dome-shaped.

A similar approach has been adopted here for the southern Benguela in order to link quantitatively the performance of the anchovy fishery with upwelling. In this study, the proxy for upwelling was annual potential new production (i.e. regional supply of NO_3-N), derived from satellite imagery and short-term coastal sea level fluctuations (Waldron *et al*. 1997). The variables chosen to examine the performance of the fishery were spawner biomass and recruitment biomass. This work was conducted with the aim of examining the OEW hypothesis in the context of the southern Benguela and ultimately to provide information of use to the management of the South African pelagic fishery .

MATERIAL AND METHODS

New production and anchovy spawner biomass

Anchovy spawner biomass has been measured acoustically each November since 1984 (Hampton 1992). The annual potential new production estimates reported by Waldron *et al.* (1997) consider the decade 1980/81–1989/90. Prior to 1984, the total allowable catch (*TAC*) of anchovy was estimated from *cpue* indices and virtual population analysis (VPA) of commercial catch data. However, research surveys conducted from 1984 rendered the catch data between 1981 and 1983 unreliable. Duncombe-Rae *et al*. (1992) demonstrated a graphically convincing relationship between the percentage of anchovy (by mass) in gannet diet and anchovy spawner biomass for the period 1984 – 1990. This relationship was extended in time and was significant (Crawford *et al*. in prep). The regressed values of anchovy biomass between 1981 and 1983 from Crawford *et al*. (in prep.) and the acoustically measured November values between 1984 and 1990 from Hampton (1992) were plotted against the annual potential new production estimates for the previous June–May periods. The life cycle of anchovy dictates that they have been exposed to environmental conditions in the southern Benguela during this period.

New production and recruitment

Hampton (1992) described the biomass of anchovy recruits from acoustic surveys taken in May, June or July along the South African west and south coasts and showed their distribution to be concentrated mainly in the southern Benguela. In this study, recruitment biomasses for each year between 1985 and 1990 were plotted against the annual potential new production

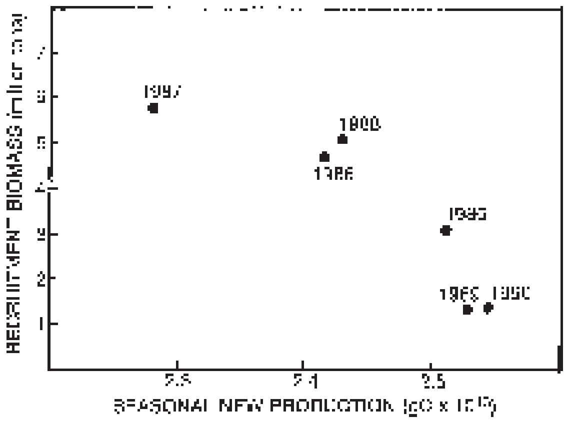

Fig. 3: Relationship between potential new production during the austral summer and autumn (December – May) and survey estimates of recruitment biomass, 1985–1990

estimated for 1984/85–1989/90 (i.e. the 12-month period preceding the acoustic surveys). Given that anchovy eggs and larvae are transported northwards from the Agulhas Bank along the West Coast during summer and autumn (December–May), the effect of upwelling on recruitment biomass was examined by focussing on the period during which eggs and larvae were most susceptible to advective loss. Therefore, the recruitment biomass for each year between 1985 and 1990 was plotted against the estimated cumulative potential new production for the summer and autumn periods preceding the acoustic estimates.

RESULTS

New production and anchovy spawner biomass

The relationship between annual potential new production for the June–May period of each year between 1980/81 and 1989/90 and the acoustically measured anchovy spawner biomass during November provided good evidence of a dome-shaped curve, supporting the OEW hypothesis (Fig. 1). The proportion of one-year-old fish in the anchovy spawner stock between 1984 and 1990 varied between 62 and 95% (B. A. Roel, Sea Fisheries Research Institute, pers. comm.). The lowest proportion was in 1989, the year of a recruitment failure (see below), when fewer one-year-olds would be expected. The mean proportion, excluding 1989, was 87%. Because almost all the spawner biomass consisted of one-year-old fish, it was not necessary to apportion *pro rata* the potential new production over the number of year-classes in the biomass estimate. A Gaussian area curve was fitted to the data (excluding the 1989 coordinate for reasons discussed later), described by the following equation:

$$y = 1.90e^{[-0.5((x-5.72)/0.43)^2]} \ (r^2 = 0.90) \quad .$$

New production and recruitment

Annual estimates of potential new production in the year preceding recruitment v. recruitment gave an indication of a similar dome-shaped relationship, with the exclusion of the 1989 coordinate (Fig. 2). The regression between summer and autumn potential new production and the ensuing recruitment biomass (Fig. 3) showed a non-linear, negative relationship, which suggested that high potential new production (or persistent upwelling) during that period was detrimental to anchovy recruitment. In that case, the 1989 coordinate was not an outlier.

DISCUSSION

The present results have demonstrated a combination of probable and possible links between upwelling (potential new production) in the southern Benguela and key variables in the pelagic fishery relating to anchovy biomass. The relationship found between annual potential new production and spawner biomass of anchovy (Fig. 1) provided strong support for the OEW hypothesis described by Cury and Roy (1989) and Roy *et al.* (1992). A subjective positioning of the OEW seems to indicate that an annual potential new production of between 5.4 and 6.1 × 10^{13} gC·year^{-1} is required for best results in the fishery. The estimates of annual potential new production were derived from remotely-sensed SST and the relationship between SST and integrated NO_3-N extended to an annual scale via the fluctuation of sea level at the coast (Waldron *et al.* 1997). Extending event-scale estimates to the annual scale relied upon the relationship between NO_3-N per event and the sea level rise at the coast associated with the propagation of the events. Although the sample number was small, the significant relationship provided a convenient currency (potential new production, gC·year^{-1}) with which to estimate cumulative annual upwelling, and the validity of the correlation was tested using published regional values and measured rates of NO_3-N supply. However, it should

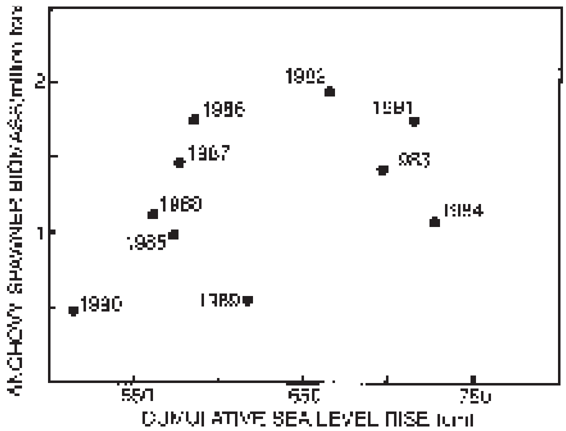

Fig. 4: Relationship between cumulative sea level rise in designated 12-month periods between 1980 and 1990 and survey estimates of anchovy spawner biomass, 1981–1990

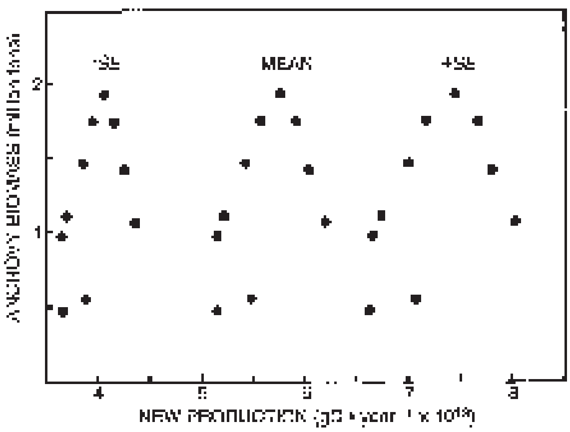

Fig. 5: Relationship between the mean and extreme (± one standard error) of the relationship between estimates of annual potential new production and survey estimates of anchovy spawner biomass

be noted that the relationship between NO_3-N and sea level rise per event is not a pre-requisite for demonstrating support of an OEW hypothesis. When only the cumulative value for sea level rise events per 12-month period (which is essentially a relative measure of coastal dynamics dominated by upwelling) was regressed against anchovy biomass, a similar dome-shaped curve was achieved, with the years retaining their relative positions on the curve (Fig. 4).

Because the decade of the 1980s was a period of high variability in the Benguela system, with substantial changes in the abundance of anchovy (Shannon *et al*. 1992), the data points covered a large portion of the dome-shaped curve. The estimates of potential new production were essentially an index of upwelling, expressed in terms of the amount of NO_3-N made available to the southern Benguela, which clearly shows that too little or too much upwelling is detrimental to anchovy biomass.

In Figures 1 and 2, the 1989 coordinate was perceived as an outlier and was therefore excluded from arguments presented in favour of a dome-shaped curve. The collapse in recruitment during that year was reported by Anon. (1989, 1991). Duncombe-Rae *et al*. (1992) suggested that the interaction of Benguela frontal waters with an Agulhas ring was a possible causative mechanism, whereby extraction of a large volume of upwelling-derived water over a period of 2–3 months removed anchovy larvae and pre-recruits from the southern Benguela at a scale sufficient to affect the overall population. Hutchings (1992) and Peterson *et al*. (1992) have reported alternative (or additional) reasons for the 1989 collapse in anchovy recruitment: feeding conditions had been poor on the western Agulhas Bank which, combined with high rates of atresia, may have resulted in an early termination of spawning.

Potential new production was relatively high in the summer and autumn of 1989 and 1990 (Fig. 3). Over the 10-year period, potential new production in the first half of the designated year (June–November) had a mean value of 2.98×10^{13} gC (range $2.60 - 3.25 \times 10^{13}$ gC). In 1988/89 (1989 recruitment) potential new production was 2.94×10^{13} gC (about average), whereas in 1989/90 (1990 recruitment) it was below average at 2.60×10^{13} gC. This may explain the relative positions of the 1989 and 1990 data points in Figures 1 and 2, but it may imply that plotting potential new production during a pivotal part of the year v. recruitment biomass is an additional avenue of future research.

It is necessary here to address the question of attributing error bars to the data points on Figure 1. The standard error relating to estimates of spawner biomass have been calculated by Hampton (1992). However, the question of error bars for the estimates of annual potential new production needs careful consideration in order to avoid a misrepresentation of the data.

The estimates of annual potential new production (Waldron *et al*. 1997) had an associated standard error of ±30%, based on the alternative equations of regression. However, to plot this variance on Figure 1 in the form of error bars would be misleading. It is important to establish that the dome-shaped relationship between annual potential new production and spawner biomass is robust to the inclusion of variance in estimates of the former.

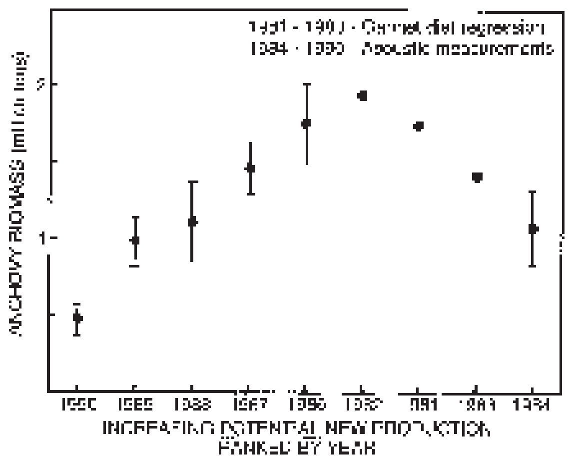

Fig. 6: Relationship between estimates of annual potential new production (ranked in increasing order and labelled according to year) and survey estimates of anchovy spawner biomass, 1981–1990. Error bars on survey estimates represent one standard error (not available for estimates of anchovy biomass derived from gannet diet regressions)

The regression equation used to predict potential new production in that study was

$$y = 0.46(\pm 0.17)x + 6.57(\pm 1.58) \quad ,$$

where y is the amount of NO_3-N per upwelling event (mmol$\times 10^{12}$) and x is the rise in sea level at the coast per upwelling event.

If the years are ranked in terms of increasing annual potential new production, then the ranking is fixed, provided the slope is positive (which is the present case). Therefore, a prediction of annual potential new production at some point on its error bar constrains the other predictions to analogous points on their respective error bars and maintains the dome shape of the curve. This is illustrated in Figure 5, where the mean and extreme predictions of annual potential new production have been plotted against anchovy biomass.

Ranked values of annual estimates of potential new production (in ascending order and labelled by year) have been substituted in Figure 6, which also includes the standard error bars for spawner biomass. It provides an alternative, non-parametric (concerning annual potential new production) method of predicting spawner biomass. For example, if an estimate of annual potential new production fell between the 1985 and 1988 values, the prediction of anchovy spawner biomass would lie somewhere in the trapezium described by the limits of those biomass error bars.

The dome-shaped curve obtained from annual potential new production and spawner biomass (Fig. 1) demonstrated that the OEW hypothesis was applicable to the southern Benguela during the decade 1981–1990. Further work will be directed towards the post-1990 period in order to extend the dataset and, in future, to provide a means of using the relationship as a predictor of anchovy (or pelagic) biomass at the end of May in any given year.

The OEW hypothesis was not as clearly demonstrated for recruitment and annual potential new production (Fig. 2). However, it is possible that, taking into account the life history of the anchovy, annual potential new production was set at a temporal scale that was too broad. The seasonal potential new production during a vulnerable period of the anchovy life cycle (Fig. 3) indicated that too much dynamic activity was detrimental to subsequent recruitment. The estimates of potential new production were timed to coincide with a period when eggs, larvae and pre-recruits were being transported up the West Coast to their recruitment grounds, when they would be most susceptible to advective loss.

The present findings improve understanding of the interlinked physical and biological functioning of the southern Benguela upwelling system. A physical index of dynamic activity in a system dominated by upwelling and manifest through the annual supply of NO_3-N (Waldron *et al.* 1997) was related to certain aspects of the pelagic fishery. Too little or too much upwelling is detrimental to the fishery, in agreement with the OEW hypothesis, but using a different independent variable. Quality of upwelling, as opposed to upwelling *per se*, has now been shown as relevant to the southern Benguela. The non-linearity of the OEW curve in Ekman-type upwelling systems (having used wind speed as a proxy for upwelling) was attributed by Cury and Roy (1989) to low food production described by the left side of the curve, as a result of the frequent absence of dynamic physical processes. Excess turbulence, defined by the right side of the curve, would result in the desegregation of food assemblages. Other factors contributing to excess upwelling, such as strong and frequent advection, would increase offshore transport and impact on food availability.

The setting of anchovy fishing quotas is currently a two-stage process, primarily governed by the results of acoustic surveys, and designed to accommodate some of the industry's operational constraints. A total allowable catch (*TAC*) is set at the beginning of a calendar year, based on acoustic estimates of anchovy spawner biomass obtained in November of the preceding year. The *TAC* may be revised, based on estimates of anchovy recruitment strength obtained in May/June. At present, the results of this study do not permit the prediction of anchovy spawner or recruitment biomass. This limitation is attributable to a combination of time-series length and operational difficulties in obtaining and processing sea level data. The next phase of this work may make it possible to make such predictions, in which case they could supplement the present management procedure for anchovy by providing an early warning of biomass fluctuations and be reflected in the planning of surveys. Such information could also add confidence to the acoustic estimates and be incorporated in a suite of operational methods for the setting of anchovy quotas.

ACKNOWLEDGEMENTS

This work was conducted with the support of the Benguela Ecology Programme and the Department of Oceanography, University of Cape Town. Liaison with the Sea Fisheries Research Institute (SFRI) is gratefully acknowledged. We are indebted to Drs L. Hutchings (SFRI) and C. Roy (Centre ORSTOM de Brest, France) for their comments and helpful suggestions on an earlier draft of this manuscript.

LITERATURE CITED

ANON. 1989 — Anchovy recruitment poor, season closes. *S. Afr. Shipp. News Fishg Ind. Rev.* **44**(4): p. 22.

ANON. 1991 — An investigation into the causes of the recent fluctuations in pelagic fish stocks off South Africa. Unpublished Report, Sea Fisheries Research Institute, South Africa: 8 pp. + 18 Figures (mimeo).

ARMSTRONG, M. J., SHELTON, P. A. and R. M. PROSCH 1985 — Catch-based assessments of population size variability of pelagic fish species exploited in ICSEAF Division 1.6. *Colln scient. Pap. int. Commn SE. Atl. Fish.* **12**(1): 17–29.

CRAWFORD, R. J. M. 1980 — Seasonal patterns in South Africa's Western Cape purseseine fishery. *J. Fish Biol.* **16**(6): 649–664.

CRAWFORD, R. J. M. 1981 — Distribution, availability and movements of anchovy *Engraulis capensis* off South Africa, 1964 – 1976. *Fish. Bull. S. Afr.* **14**: 51–94.

CRAWFORD, R. J. M., SHELTON, P. A., BERRUTI, A. and J. A. A. DE OLIVEIRA (in preparation) — Diet of Cape Gannets *Morus capensis* as an estimator of abundance of Cape anchovy *Engraulis capensis* off South Africa.

CURY, P. and C. ROY 1989 — Optimal environmental window and pelagic fish recruitment success in upwelling areas. *Can. J. Fish. aquat. Sci.* **46**(4): 670–680.

DUNCOMBE-RAE, C. M., BOYD, A. J. and R. J. M. CRAWFORD 1992 — "Predation" of anchovy by an Agulhas ring: a possible contributory cause for the very poor year-class of 1989. In *Benguela Trophic Functioning*. Payne, A. I. L., Brink, K. H., Mann, K. H. and R. Hilborn (Eds). *S. Afr. J. mar. Sci.* **12**: 167–173.

HAMPTON, I. 1987 — Acoustic study on the abundance and distribution of anchovy spawners and recruits in South African waters. In *The Benguela and Comparable Ecosystems*. Payne, A. I. L., Gulland, J. A. and K. H. Brink (Eds). *S. Afr. J. mar. Sci.* **5**: 901–917.

HAMPTON, I. 1992 — The role of acoustic surveys in the assessment of pelagic fish resources on the South African continental shelf. In *Benguela Trophic Functioning*. Payne, A. I. L., Brink, K. H., Mann, K. H. and R. Hilborn (Eds). *S. Afr. J. mar. Sci.* **12**: 1031–1050.

HUTCHINGS, L. 1992 — Fish harvesting in a variable, productive environment - searching for rules or searching for exceptions? In *Benguela Trophic Functioning*. Payne, A. I. L., Brink, K. H., Mann, K. H. and R. Hilborn (Eds). *S. Afr. J. mar. Sci.* **12**: 297–318.

IVERSON, R. L. 1990 — Control of marine fish production. *Limnol. Oceanogr.* **35**(7): 1593–1604.

JAMES, A. G. 1987 — Feeding ecology, diet and field-based studies on feeding selectivity of the Cape anchovy *Engraulis capensis* Gilchrist. In *The Benguela and Comparable Ecosystems*. Payne, A. I. L., Gulland, J. A. and K. H. Brink (Eds). *S. Afr. J. mar. Sci.* **5**: 673–692.

MENDELSSOHN, R. 1989 — Reanalysis of recruitment estimates of the Peruvian anchoveta in relationship to other population parameters and the surrounding environment. In *The Peruvian Upwelling Ecosystem: Dynamics and Interactions*. Pauly, D., Muck, P., Mendo, J. and I. Tsukayama (Eds). *ICLARM Conf. Proc.* **18**: 364–385.

ORBI, A., ROY, C., CURY, P. and S. BENCHERIFI 1991 — Abondance apparente des sardines marocaines de la zone A et variabilité du recrutement. In *Pêcheries Ouest Africaines: Variabilité, Instabilité et Changement*. Cury, P. and C. Roy (Eds). Paris; ORSTOM: 439–445.

PETERSON, W. T., HUTCHINGS, L., HUGGETT, J. A. and J. L. LARGIER 1992 — Anchovy spawning in relation to the biomass and the replenishment rate of their copepod prey on the western Agulhas Bank. In: *Benguela Trophic Functioning*. Payne, A. I. L., Brink, K. H., Mann, K. H and R. Hilborn (Eds). *S. Afr. J. mar. Sci.* **12**: 487–500.

ROY, C., CURY, P. and S. KIFANI 1992 — Pelagic fish recruitment success and reproductive strategy in upwelling areas: environmental compromises. In *Benguela Trophic Functioning*. Payne, A. I. L., Brink, K. H., Mann, K. H. and R. Hilborn (Eds). *S. Afr. J. mar. Sci.* **12**: 135–146.

SHANNON, L. V., CRAWFORD, R. J. M., POLLOCK, D. E., HUTCHINGS, L., BOYD, A. J., TAUNTON-CLARK, J., BADENHORST, A., MELVILLE-SMITH, R., AUGUSTYN, C. J., COCHRANE, K. L., HAMPTON, I., NELSON, G., JAPP, D. W. and R. J. Q. TARR 1992 — The 1980s – a decade of change in the Benguela ecosystem. In *Benguela Trophic Functioning*. Payne, A. I. L., Brink, K. H., Mann, K. H. and R. Hilborn (Eds). *S. Afr. J. mar. Sci.* **12**: 271–296.

SHELTON, P. A. 1986 — Fish spawning strategies in the variable southern Benguela Current region. Ph.D. thesis, University of Cape Town: [vi] + 327 pp.

SHELTON, P. A. and L. HUTCHINGS 1982 — Transport of anchovy, *Engraulis capensis* Gilchrist, eggs and early larvae by a frontal jet current. *J. Cons. perm. int. Explor. Mer* **40**(2): 185–198.

WALDRON, H. N., PROBYN, T. A. and G. B. BRUNDRIT 1997 — Preliminary annual estimates of regional nitrate supply in the southern Benguela using coastal sea level fluctuations as a proxy for upwelling. *S. Afr. J. mar. Sci.* **18**: 93–105.

WARE, D. M. and E. THOMPSON 1991 — Link between long-term variability in upwelling and fish production in the northeast Pacific Ocean. *Can. J. Fish. aquat. Sci.* **48**(12): 2296–2306.