



Observations on the distribution and relative abundance of the scyphomedusan *Chrysaora hysoscella* (Linné, 1766) and the hydrozoan *Aequorea aequorea* (Forskål, 1775) in the northern Benguela ecosystem

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Abstract

Observations on the abundance of medusae at the surface were conducted in the northern Benguela ecosystem, over the period August 1997–June 1998. The results suggest that *Chrysaora hysoscella* is found inshore, whereas *Aequorea aequorea* tends to be found offshore. Although these relative observations are subject to bias caused by seasonal changes in the survey area, they are generally supported by the results of correlation analyses, and by the results of a more quantitative, cross-shelf trawl survey. Both species of medusae display marked patchiness, and can be very abundant. They appear to have mostly non-overlapping patterns of distribution in the upper layers of the water column, and so are able to exert a consistent predation pressure across the width of the continental shelf. The estimates of biomass obtained are used as input variables to existing models of energy flow within the ecosystem.

Introduction

The Benguela ecosystem is one of the major upwelling areas of the world, and extends from northern Namibia (~17 °S), to south of Cape Point in South Africa (34 °S). The Luderitz upwelling cell (~27 °S) represents a natural internal boundary to the system, and the areas to either side are referred to as the northern and southern Benguela (Shannon, 1985). The waters of the northern Benguela are less markedly seasonal than they are in the south (Shannon, op. cit.; Estrada & Marrasé, 1987), and support a higher biomass owing to the less dynamic oceanography (Brown et al., 1991).

Although the dominant large medusae currently observed in the northern Benguela ecosystem are the scyphomedusan *Chrysaora hysoscella* (Linné, 1766)

and the hydromedusan *Aequorea aequorea* (Forskål, 1775), the detailed plankton studies that were conducted in the region during the 1950s (Hart & Currie, 1960) and 1960s (Stander & De Decker, 1969) did not report the presence of either species. *C. hysoscella* and *A. aequorea* were first noted in the early 1970s by King & O'Toole (1973), Cram & Visser (1973) and Schülein (1974) during their investigations on commercially important fishes. These studies did not examine either *C. hysoscella* or *A. aequorea* in any detail, however, and the first quantitative studies were only forthcoming some 15 years later (Venter, 1988; Fearon et al., 1992). Although both these latter studies reported on the abundance of large medusae in the region, they were based either on incidental statistics collected from the fishing industry (Venter, op. cit.), or from small-mouth Bongo nets (Fearon et al., op

cit.). Both data sets are therefore, biased – the former by the problems attendant with fisheries dependent data (e.g. selective operational area, marked seasonality and poor records), and the latter by inadequate sampling. As a consequence they can only provide data of a relative nature. The most rigorous study of medusae in the northern Benguela was conducted by Pagès (1991), and it focused on small (principally hydro-) medusae that were collected by bongo nets. Despite the disparate methods that have hitherto been employed to study medusae in the region, they all agree on the dominant species present and on their general pattern of distribution.

The apparent increase in large medusae that has been observed in the northern Benguela ecosystem has been observed elsewhere in the world (Mills, 2001). Brodeur et al. (1999) documented a substantial increase in gelatinous zooplankton in the Bering Sea over the last 20 years, and Graham (2001) noted an increase in the abundance of *Chrysaora quinquecirrha* and *Aurelia aurita* in the Gulf of Mexico. A number of explanations have been put forward to explain these increases including climate change (Mills, 2001), eutrophication (Arai, 2001) and overfishing (Purcell & Arai, 2001).

Medusae are carnivorous, and can have negative impacts on zooplankton populations (e.g., Behrends & Schneider, 1995; Feigenbaum & Kelly, 1984; Purcell 1992) and fish eggs and larvae (reviewed in Purcell & Arai, 2001) when they occur at high densities. They are thought to have an important, if unquantified, role in the structure of pelagic ecosystems (Hernroth & Gröndahl, 1983). In the Benguela ecosystem, large medusae spoil and reduce fish catches, and are thought to interfere with the hydroacoustic assessment of pelagic fish stocks (Brierley et al., 2001; D. Boyer, NatMIRC, Swakopmund, pers. comm.). Although medusae are clearly important from an ecosystem and commercial point of view, the general decline in funds for ocean-going research in southern Africa has meant that studies on species of no direct commercial value have become limited. Research efforts directed towards medusae have, therefore, been of low priority, and have been conducted mainly opportunistically. The studies presented here are of such a nature, and deal largely with cross-shelf and alongshore patterns of distribution determined from observations of medusae at the surface that were conducted aboard cruises of opportunity.

Materials and methods

Observations of *C. hysoscella* and *A. aequorea* were made from the bow of the RV *Welwitschia* between August 1997 and June 1998. The data were collected from six cruises in the area between 17° S and 28° S. Observations were concentrated between the Cunene River (17° 30' S) and Conception Bay (24° S) (Fig. 1a). All observations ($n = 410$) were made during the day between 07:00 and 18:00. Medusae were identified and counted within a band 5 m wide to the front of the bow, whilst the ship steamed at 10 knots. Counts were carried out for 10 minutes every hour, subject to visibility and sea-state, and these were converted to densities using knowledge of the distance steamed. When dense patches of medusae were observed within any sampling period, counts were estimated from smaller areas and then multiplied up by total patch area. No effort was made to examine patchiness within any sampling period, and so estimated density was based on the total counts per sampling period. Information on latitude, longitude, time and sea-surface temperature were recorded with each observation (sea-surface salinity was not recorded). Correlation analyses between these environmental variables and surface abundance were conducted using Statistica software. Only those data that were collected when the sea was flat and the visibility was good were used in the analyses.

Additional information on the cross-shelf distribution of large medusae was provided by a trawl survey conducted between 31 August and 6 September 1999 aboard the RV *Dr. Fridtjof Nansen*. The survey transect was situated off central Namibia (22° S), and extended between 12° 42' E (water depth 430 m) and 13° 47' E (102 m) (Fig. 1a). A total of 66 trawls were conducted using a pelagic Åkra trawl fitted with two nets of similar design. The smaller net was fitted with a Multisampler (Skeide et al., 1997) that enabled three separate samples to be collected from a single trawl, and the larger net was fitted with balloon floats that enabled surface (between 19 and 31 m) trawls to be made. The towing time varied between 2 and 15 min. The nets were towed at a speed of 3 knots. The nets had circular mouth openings of 12 m diameter, and they were fitted with a mesh that reduced in size from 400 mm diameter at the mouth, to 36 mm diameter at the cod-end. Few of the tows sampled the entire water column and most (78%) sampled within the upper 50 m only. Two trawls fished at depths greater than 200 m. CTD casts were made with a Seabird SBE 9+ probe

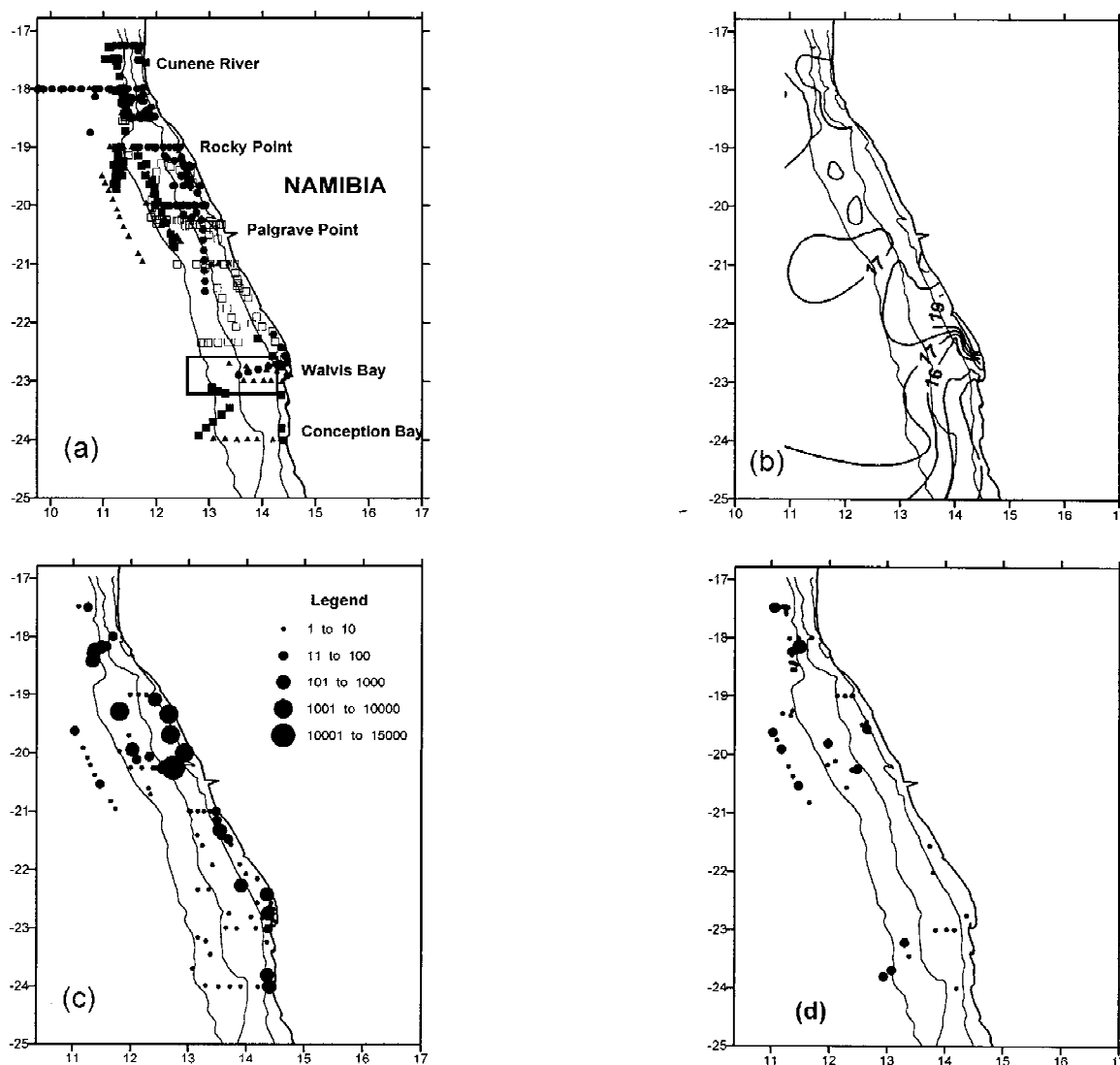


Figure 1. Study area across the Namibian shelf showing location of observation sites (\blacktriangle - spring, \square - summer, \bullet - autumn, \blacksquare - winter), and the general area of the trawl survey conducted in August/September 1999 (blocked) (a). Isotherms of mean sea surface temperature (b), and abundance (numbers per 10 minute sampling period) of *Chrysaora hysoscella* (c) and *Aequorea aequorea* (d) between August 1997 and July 1998 (data pooled). Isobaths (100 m, 200 m and 500 m) indicated in each panel.

(SBE 11+ deck unit) to near bottom at six locations along the transect. Station spacings corresponded to approximately 50 m increments in bottom depth.

Results

A total of six surveys were conducted in the area between Conception Point (24° S) and the Cunene River (17° S) (Fig. 1a), during the period August 1997 and July 1998. The study area varied between the

surveys (Fig. 1a), as did the number of observations ($N = 133$, autumn; $N = 104$, winter; $N = 89$, spring; $N = 84$, summer). Sea surface temperature (SST) varied between 10 and 22°C during the study period, and the modal SST of the samples was 17°C (Fig. 2a). The mean SST of the survey area over the course of the study period was 17.4°C , but this varied on a seasonal basis (18.68°C , summer; 17.64°C , autumn; 16.97°C , winter; 17.37°C , spring). SST was significantly affected by both latitude and longitude (stepwise mul-

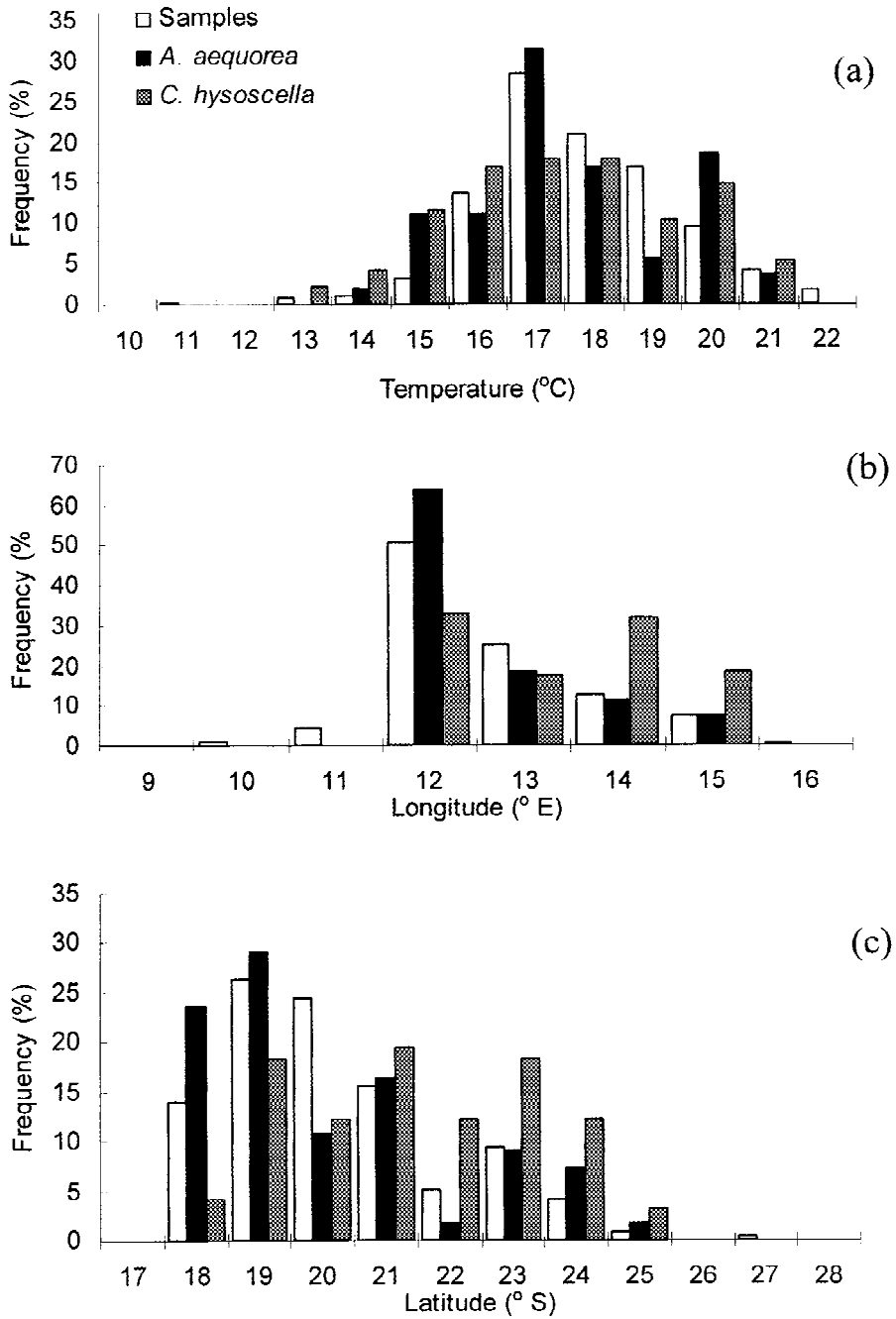


Figure 2. Distribution of *Chrysaora hysoscella* and *Aequorea aequorea* observations, within classes of (a) temperature, (b) longitude, and (c) latitude. All data pooled.

tiple regression analysis, $p < 0.0001$), and warmer water was encountered offshore and to the north.

Over the course of the year, *C. hysoscella* was recorded throughout the entire observation area (Fig. 1c) ($n = 97$). The species was characterised by gener-

ally low abundance (<10 medusae per observation) throughout the observation area but high (>100 medusae per observation) densities were recorded close to shore. Highest densities (>1000 medusae per observation) were observed inshore, between Rocky Point

(19° S) and Palgrave Point (20° 30' S). The distribution of *A. aequorea* ($n = 55$) was sparser than *C. hysoscella*, particularly in the southern regions of the observation area between 22° S and 24° S. *A. aequorea* was most abundant between Palgrave Point and the Cunene River (Fig. 1d).

Although neither species of medusae occurred in samples collected at the extremes of SST observed, *C. hysoscella* tended to be found more frequently at temperatures ≤ 16 °C (31%) than *A. aequorea* (24%) (Fig. 2a). Temperatures within this range were found in the inshore and southern waters of the study area (Fig. 1b). It would appear from the distribution of *A. aequorea* in relation to longitudinal classes, that this species occurred further offshore than *C. hysoscella* (Fig. 2b). Longitude has been used as a proxy for depth (in the absence of these data), due to the near linear coastline and narrow continental shelf within the study area. 79% of the observations of *A. aequorea* occurred north of 22 °S, as opposed to only 53% of those of *C. hysoscella* (Fig. 2c).

An analysis of the correlations between abundance and the various environmental parameters (time of observation, SST, latitude and longitude), revealed some conflicting results. When the entire data set was analysed, the only significant ($p < 0.05$) correlation was between *C. hysoscella* and observational time. An examination of the scatter-plot between observational abundance and time (Fig. 3) suggested that the numbers of *C. hysoscella* at the surface were greatest at dawn and dusk. This implied the population underwent some sort of diel vertical migration, and required that, for other trends, the data set be analysed between 08:00 and 17:00.

Analysis of the time-filtered data set was undertaken on a cruise-by-cruise basis, because each cruise was conducted at a different time of the year, had a different survey grid and collected a different number of samples (Fig. 1a). Generally, *C. hysoscella* increased in abundance to the south¹, and it was more abundant in nearshore waters (Table 1). The abundance of *C. hysoscella* was inversely correlated with SST in summer, and positively correlated with SST in winter. The abundance of *A. aequorea* showed fewer significant

Table 1. Significant (p) correlation coefficients (r) between the observed abundance (m^{-2}) of *Chrysaora hysoscella* and *Aequorea aequorea* and measured environmental variables from August 1997 to July 1998. The months for the seasons are: Winter (June and July); Spring (October); Summer (November and December) and Autumn (March and April)

Season	Variable	Species	r	P	N
Autumn	Longitude	<i>C. hysoscella</i>	0.22	0.01	131
Autumn	Latitude	<i>C. hysoscella</i>	0.21	0.02	131
Spring	Longitude	<i>A. aequorea</i>	-0.30	0.05	43
Summer	Temperature	<i>C. hysoscella</i>	0.34	0.04	36
Winter	Latitude	<i>C. hysoscella</i>	0.51	0.00	72
Winter	Temperature	<i>C. hysoscella</i>	-0.50	0.00	72
Winter	Latitude	<i>A. aequorea</i>	-0.26	0.03	72
Winter	Longitude	<i>C. hysoscella</i>	0.70	0.00	72

trends within the different seasons (Table 1). However, the abundance of *A. aequorea* was correlated negatively with both latitude and longitude, which suggests that it was more common in the north and offshore. It should be noted that the correlation coefficients were low in most cases, implying that other factors were also important in determining the abundance and distribution of both species.

The results of the trawl survey conducted during the cruise in Autumn 1999 showed that higher densities of *C. hysoscella* were found in the inner and middle regions of the shelf (<150 m), whereas *A. aequorea* was more abundant in the deeper (>150 m) offshore waters (Fig. 4). This cross-shelf pattern in the distribution of *C. hysoscella* and *A. aequorea* may reflect the strong temperature and salinity gradients (Fig. 5) that were associated with the sharp shelf-break front (between 13 and 13.1 E). The shelf-break front represented the western limit of large catches of *C. hysoscella* (>100 kg per min). Inshore of this front the water column was not well-mixed. There was a weak, sub-surface frontal feature around 13.4 E, and this, broadly speaking, coincided with the transition between catches dominated by *C. hysoscella* and *A. aequorea*. Both species were patchy in their distribution, and although most trawls were of relatively low density, some were of very high density (Fig. 6a,b). These results generally support the findings of the visual observations (Fig. 6c,d).

¹ Although these results may appear to contrast with the data illustrated in Fig. 1b (wherein higher abundances of *C. hysoscella* were observed in the northern, than southern, part of the study area), all data were pooled in the construction of this figure. The results of the correlation analyses between abundance and latitude were derived from seasonal analyses, of smaller areal data sets (Figure 1a). The high abundances observed at 20S were noted on a survey where this latitude was at the southern limit of the survey grid.

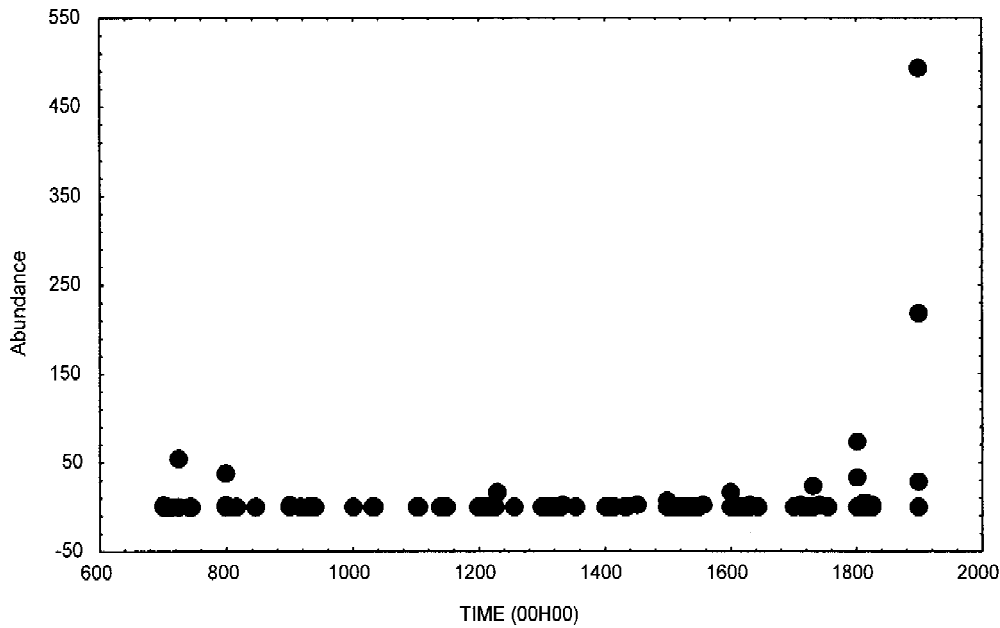


Figure 3. Density of *Chrysaora hysoscella* (m^{-2}) observed at the surface versus time of day. Only non-zero data shown; all data pooled.

Discussion

Information on the distribution and abundance of medusae that has been derived from surface observations is subject to a number of criticisms. Observations are dependent upon sea-state and visibility, reflect observer bias, and are also influenced by diel vertical migration (DVM). Despite the fact that all these variables were standardised here, our results should be interpreted as measures of relative abundance. Therefore, concordance with other data sets need not be strict. Having said that, the relative cross-shelf distribution of the two species was similar in both data sets, which lends some credibility to the use of surface observations in determining the distribution and relative abundance of large medusae. The use of surface observations in determining the relative abundance and distribution of medusae is not new, and Purcell et al. (2000) used a modified approach to estimate the density of *Aurelia labiata* aggregations in Prince William Sound.

The inferences on DVM of *C. hysoscella* made here are supported, in part, by the results of an hydroacoustic survey (Brierley et al., 2001). Those authors noted that the sound scattering layer of *C. hysoscella* (at 25 m depth) was clearly detectable during the day, but that it was less distinct at night, probably as individuals migrated upwards in the wa-

ter column, returning to depth the following day. A number of other authors have noted that species of the genus *Chrysaora* display DVM (e.g., Pagès, 1991; Schuyler & Sullivan, 1997), although few have been able to correlate the behaviour with the environment.

There was tendency within any seasonal set of samples, for *C. hysoscella* to occur inshore and in the south (Table 1). These results are consistent with the cross-shelf distribution patterns recorded by Pagès & Gili (1991), and Fearon et al. (1992). Medusae of the genus *Chrysaora* are known to exhibit seasonal patterns of abundance (Kramp, 1961). Although the life cycle of *C. hysoscella* within the region remains unknown, it has been postulated that the ephyrae released by benthic scyphistomae in the north are carried south by the inshore undercurrent (Fearon et al., op cit.). Juvenile medusae are then thought to mature on their southward journey, which results in their higher observed numbers there, than in the north². The variable response of *C. hysoscella* to temperature (Table 1) may reflect seasonality in hydrography. Inshore water temperatures during summer tend to be lower than in winter, because of upwelling, which is seasonal at these latitudes (Shannon, 1985). *C. hysoscella* might

² Unfortunately, the data sets collected here did not allow us to confirm the seasonal changes in distribution postulated by Fearon et al. (op cit.), owing to the lack of conformity in sampling area, and a lack of full-shelf coverage.

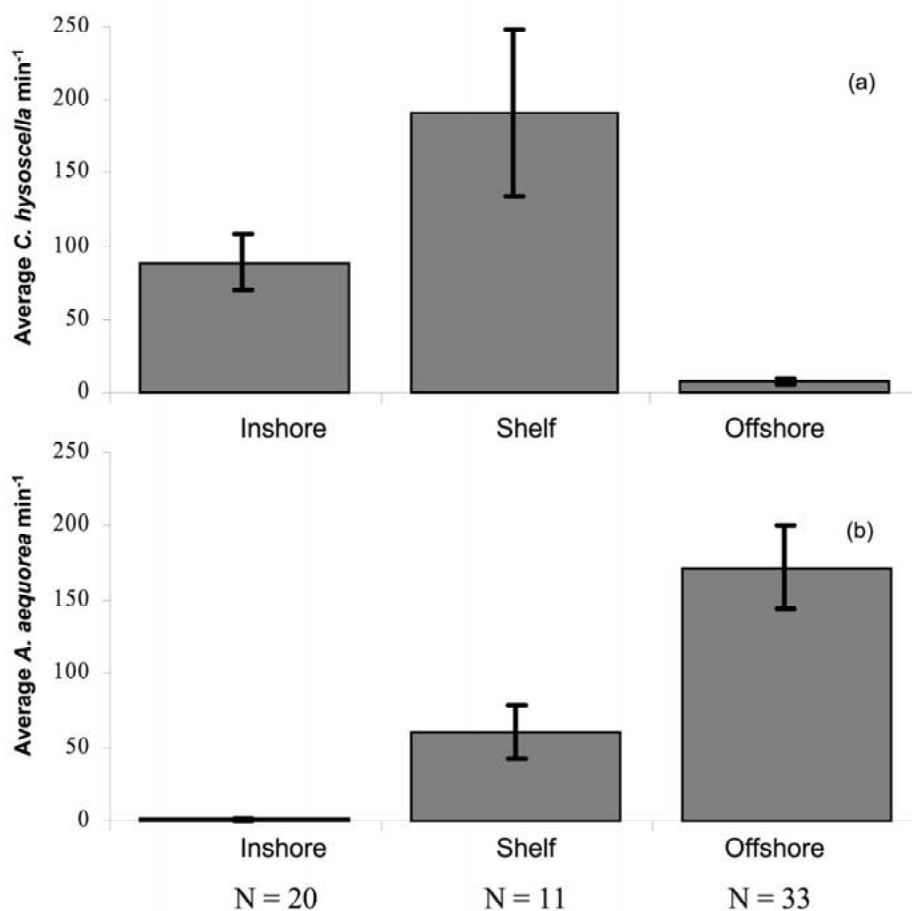


Figure 4. The mean (\pm S. E.) catch (kg min⁻¹) of (a) *Chrysaora hyoscella* and (b) *Aequorea aequorea* versus distance from shores. Number of trawls indicated; data from the cruise conducted in August/September 1999.

be considered a cold water species, but newly upwelled water is low in food and requires some level of maturation before populations of zooplankton prey begin to develop (Denman & Powell, 1984).

Although *A. aequorea* tended to be found offshore and in the north (Fig. 3), this was poorly supported by the correlation analyses, and can be attributed to their relatively low abundance. Pagès (1991) regarded *A. aequorea* as a shelf species, and found that it was particularly abundant in a broad strip separating coastal from oceanic waters. Fearon et al. (1992) reported that *A. aequorea* was common in the region between 20° S and 21° S (off Palgrave Point), but that it decreased in the areas north of 19° S and south of 24° 30' S. Our understanding of the biology of this species in the region is poor and precludes detailed comment.

The data for both species were characterised by great horizontal patchiness (Fig. 6). A number of

factors influence the horizontal distribution of medusae, including physical processes, and behavioural responses to the prevailing environment (Graham et al., 2001). Langmuir convection cells result in regularly spaced (micro- and mesoscale) patches of plankton at the surface (Boero, 1991; Larson, 1992), and have been evoked to explain patchiness in the distribution of red tides off the South African west coast (*A. Boyd, M&CM, Cape Town; unpublished data*). Elsewhere in the world, medusae have been shown to be aggregated at upwelling fronts (Graham, 1994) and in areas of flow discontinuity (Purcell et al., 2000), and may accumulate in areas influenced by wind (Axiak et al., 1991), as well as eddies, currents and tides (Arai, 1992a). Medusae show behavioural responses to their food environment (Bailey & Batty, 1983; Arai, 1992b), which may allow them to aggregate in patches of high food density.

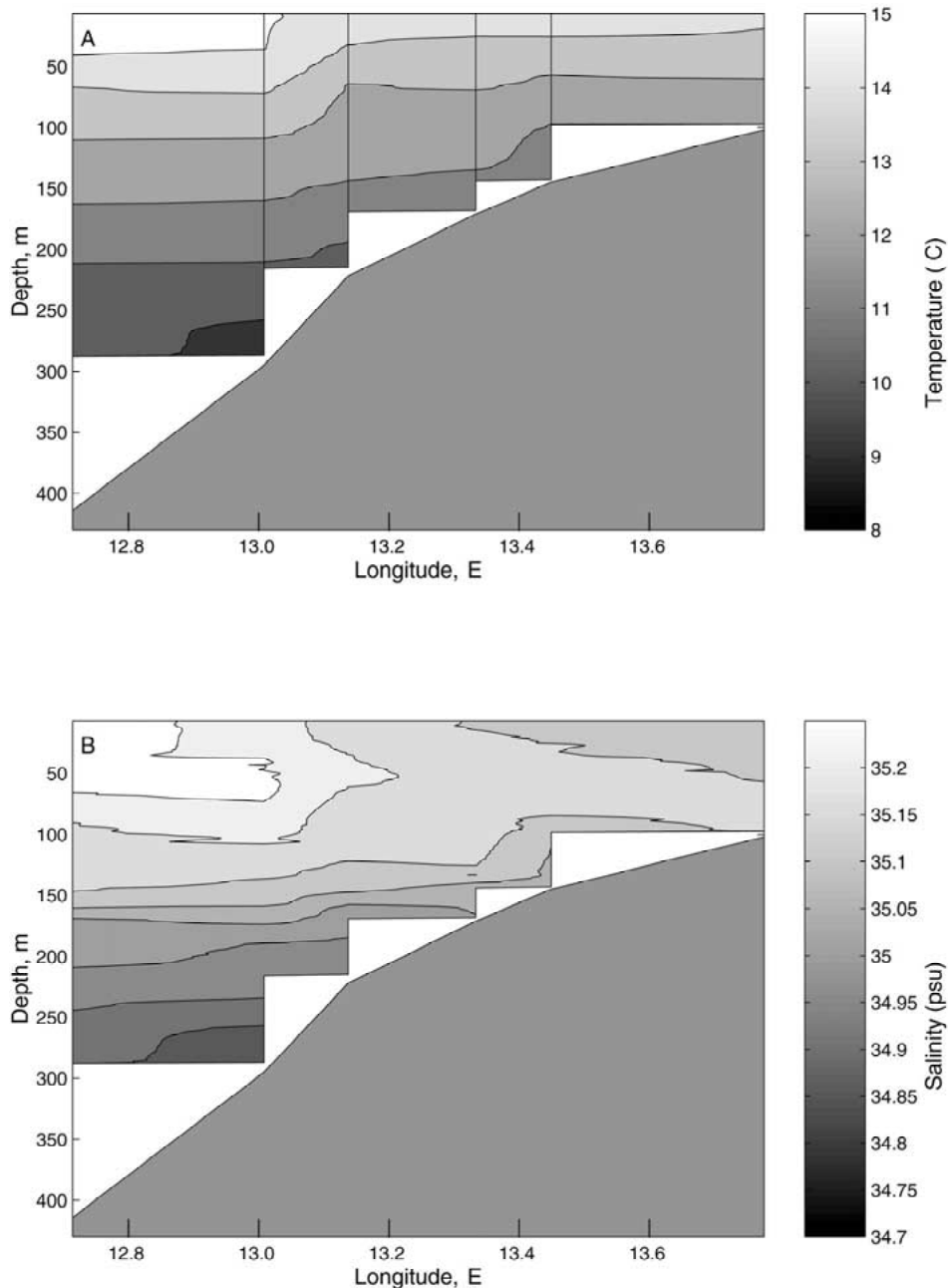


Figure 5. Vertical sections of temperature (a) and salinity (b) across the Namibian shelf at 22° S (12° 42' E to 13° 47' E), in August/September 1999. The data were collected during the trawl survey and were de-spiked prior to contouring.

One of the most significant results of this study is the apparent segregation in space between *C. hysoscella* and *A. aequorea*. This finding was common to both the observational, and the trawl data sets (Fig. 7), and suggests that the one species only occurred at high numbers when the other was rare. In his analysis of cnidarian assemblages in the region, Pagès (1991) as-

signed the two species to different water masses (*A. aequorea* – shelf, *C. hysoscella* – coastal-shelf) but did not comment further. A negative relationship between the abundance of the *C. hysoscella* and *A. aequorea* could be interpreted in terms of predation, because both genera are known to include pelagic coelenterates in their diet (Russell, 1970; Purcell, 1991). How-

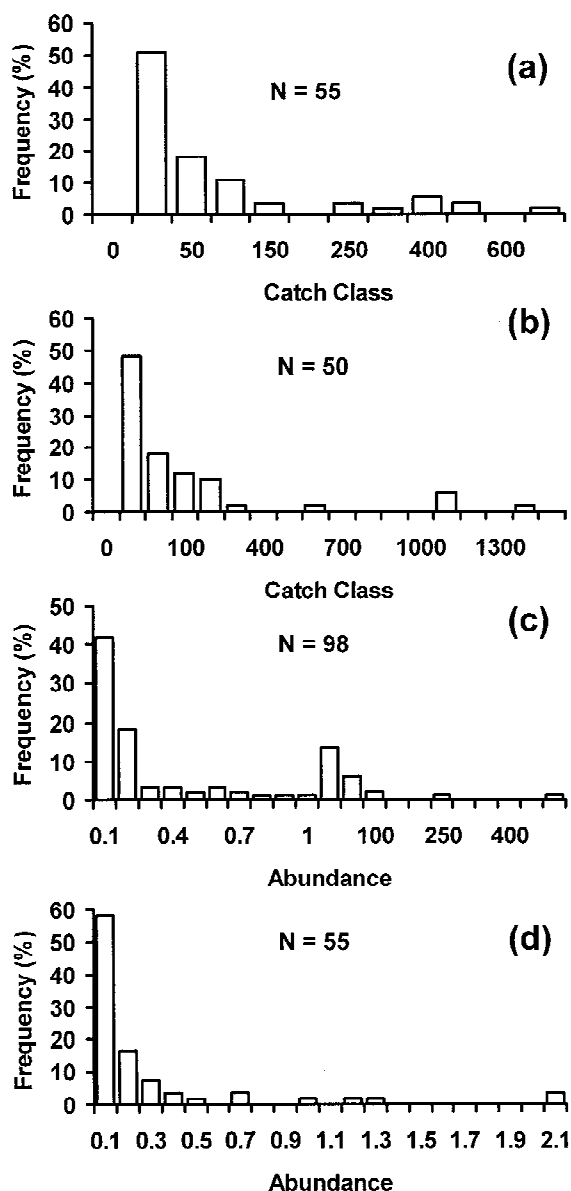


Figure 6. Frequencies (%) of observational density and catch abundance of *Chrysaora hysoscella* (a,c) and *Aequorea aequorea* (b,d). Trawl data (as kg min^{-1} , a,b), observational data (numbers 1000 m^{-2} , c,d).

ever, the absence of a negative relationship in this instance could imply some sort of spatial partitioning. Although this conclusion is based on data collected in the upper layers of the water column, and does not take cognisance of any deep-water populations, it is nevertheless valid over that depth range. Should there be deeper-living populations of either species, then this partitioning has an additional vertical component.

The 'partitioning' of horizontal and vertical space has been observed in other zooplankton from the Benguela ecosystem (Gibbons & Hutchings, 1996). Barange (1990) noted cross-shelf changes in the euphausiid assemblage in the northern Benguela, whilst Gibbons (1994) observed cross-shelf and vertical segregation of the dominant chaetognaths. It has been suggested that these examples of spatial partitioning might reflect competition (or the 'ghost of competition past'), and a similar explanation can be invoked here, as species of both genera eat a variety of hard- and soft-bodied zooplankton (Purcell, 1991; Purcell & Cowan, 1995; Purcell & Sturdevant, 2001).

This explanation would require that both species be able to identify some sort of environmental feature that would act as a boundary to their centres of preferred distribution. The front may represent just such a feature, because the catches of medusae in the trawl survey were not related to its position directly, but rather it acted as a boundary between the two species. This interpretation of the results implies that there is some biological structure to the assemblage of large medusae in the northern Benguela ecosystem, as has been postulated for cnidarians in the Mediterranean Sea (Buecher & Gibbons, 1999), and for other zooplankton assemblages in the southern Benguela ecosystem (Gibbons et al., 1999).

Whatever the underlying cause for the spatial partitioning of the waters of the northern Benguela region, it results in the distribution of large medusae across the regional shelf. A spatially persistent level of predation pressure is, therefore, applied across the shelf, the impact of which will depend upon the rate processes and biomass estimates of predator and prey. The trawl data derived from the *Dr. Fridtjof Nansen* survey represent the first estimates of large medusae abundance for the region, and therefore have value as input parameters for models of ecosystem functioning. A simple mass-balance model (Ecopath – Christensen & Pauly, 1992) has been used locally to explore ecosystem functioning (Jarre-Teichmann et al., 1998; Shannon & Jarre-Teichmann, 1999), and the results suggest that medusae play a negligible role in the system. Although the estimate of biomass employed in the model ($\sim 5 \times 10^6$ tons) was little more than a guess (L. Shannon, M&CM, Cape Town, pers. comm.), the refined estimate generated here³ differs little from it. It is estimated from the mean catch data that a total of 4.9 million

³ Using mean catch data and assuming that both species are homogeneously distributed across the entire $179\,000 \text{ km}^2$ of the northern Benguela.

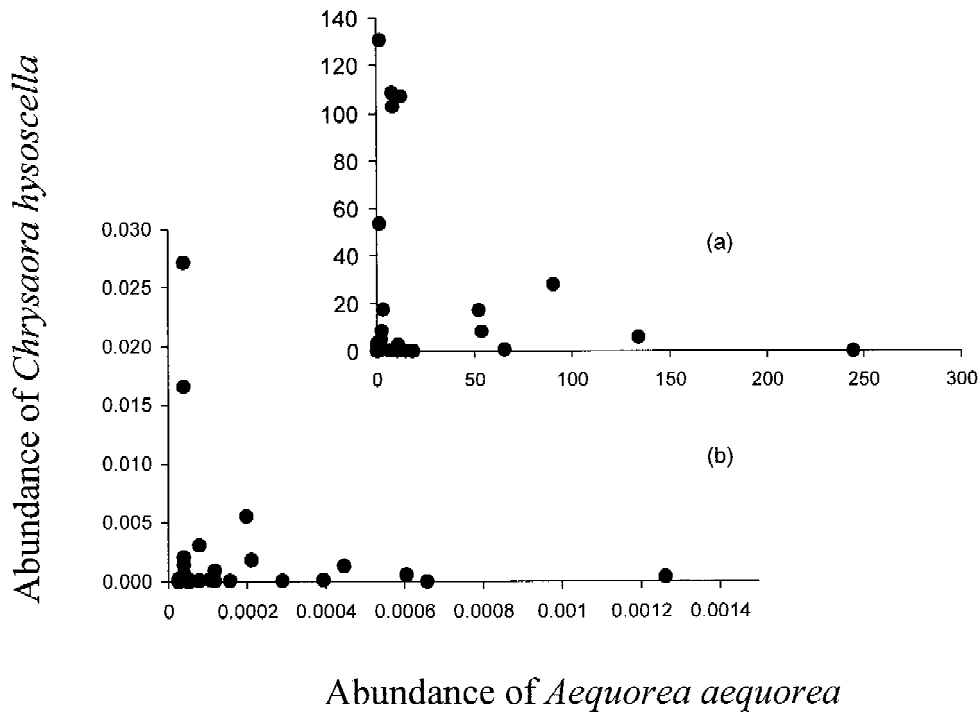


Figure 7. The relationship between the abundance of *Chrysaora hysoscella* and *Aequorea aequorea*, in the northern Benguela. Data from trawl surveys conducted in August/September 1999 (a) – as kg min^{-1} , and observations (b) – as numbers m^{-2} . Only non-zero data shown; all data pooled.

tons of medusae may occur in the region (1.8×10^6 tons *C. hysoscella*, 3.1×10^6 tons *A. aequorea*). It should be realised that these data were collected over a one-week period during winter. Consequently, the estimate should be viewed with caution. However, if the maximum densities of medusae are used as input parameters (13.1×10^6 tons *C. hysoscella* and 22.3×10^6 tons *A. aequorea*), the model becomes unbalanced and it is clear that medusae play a very significant role within the system (L. Shannon, M&CM, Cape Town, pers. comm.). An expansion of the model, as it pertains to medusae, falls outside the scope of this paper. Rather, we believe that the model needs to be re-visited, and greater attention needs to be paid to the estimates of production and ingestion used, as well as to the biomass values employed. We would ultimately anticipate that the significance of medusae will lie somewhere between the two extremes, though this is likely to vary on a seasonal basis.

The persistent decline in financial support for research into species of no commercial value in southern Africa, means that alternative methods for collecting data on these species will become more important. These alternative methods include beach-surveys

of stranded specimens, the use of offshore drilling-platforms to collect samples and to make daily observations. They also include participation on cruises (research, fishing, etc.) of opportunity, and analyses of commercial fishing returns. Such methods were employed by Axiak et al. (1991), Benović (1991) and Carli (1991) for medusae in the Mediterranean Sea, and they proved to be relatively successful, despite their limited scope. Although the observational data collected here on cruises of opportunity were of a relative nature, they were supported (in part) by the results of a dedicated cruise, which suggests that the technique can be more widely applied.

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References

- Arai, M. N., 1992a. Active and passive factors affecting aggregations of hydromedusae: a review. *Sci. mar.* 56: 99–108.
- Arai, M. N., 1992b. Attraction of *Aurelia* and *Aequorea* to prey. *Hydrobiologia* 216/217: 363–366.
- Arai, M. N., 2001. Pelagic coelenterates and eutrophication: a review. *Hydrobiologia* 451 (Dev. Hydrobiol. 155): 69–87.
- Axiak, V., C. Galea & P. J. Schrembri, 1991. Coastal aggregations of the jellyfish *Pelagia noctiluca* (Scyphozoa) in Maltese coastal waters during 1980–1986. Proceedings of the 2nd Workshop on Jellyfish Blooms in the Mediterranean Sea. UNEP, Athens. Map tech. Rep. Ser. 47: 32–40.
- Bailey, K. M. & R. S. Batty, 1983. Laboratory study of predation by *Aurelia aurita* on larval herring (*Clupea harengus*): experimental observations compared with model predictions. *Mar. Biol.* 72: 295–301.
- Barange, M., 1990. Vertical migration and habitat partitioning of six euphausiid species in the northern Benguela upwelling system. *J. Plankton Res.* 12: 1223–1237.
- Behrends, G. & G. Schneider, 1995. Impact of *Aurelia aurita* medusae (Cnidaria, Scyphozoa) on the standing stock and community composition of mesozooplankton in the Kiel Bight (western Baltic Sea). *Mar. Ecol. Prog. Ser.* 127: 39–45.
- Benović, A. F., 1991. The aspect of jellyfish distribution in the Adriatic. Proceedings of the 2nd Workshop on Jellyfish Blooms in the Mediterranean Sea. UNEP, Athens. Map tech. Rep. Ser. 47: 41–50.
- Boero, F., 1991. Contribution to the understanding of blooms in the marine environment. Proceedings of the 2nd Workshop on Jellyfish Blooms in the Mediterranean Sea. UNEP, Athens. Map tech. Rep. Ser. 47: 72–76.
- Brierley, A. S., B. E. Axelsen, E. Buecher, C. A. J. Sparks, H. Boyer & M. J. Gibbons, (2001). Acoustic observations of jellyfish in the Namibian Benguela. *Mar. Ecol. Prog. Ser.* 210: 55–66.
- Brodeur, R. D., C. E. Mills, J. E. Overland, G. E. Walters & J. D. Schumacher, 1999. Evidence for a substantial increase in gelatinous zooplankton in the Bering Sea, with possible links to climate change. *Fish. Oceanogr.* 8: 296–306.
- Brown, P. C., S. J. Painting & K. L. Cochrane, 1991. Estimates of phytoplankton and bacterial biomass and production in the northern and southern Benguela ecosystems. *S. Afr. J. mar. Sci.* 11: 537–564.
- Buecher, E. & M. J. Gibbons, 1999. Temporal persistence in the vertical structure of the assemblage of planktonic medusae in the NW Mediterranean Sea. *Mar. Ecol. Prog. Ser.* 189: 105–115.
- Carli, A., 1991. Macroplanktonic jellyfish in the Ligurian Sea (1984–1986). Monitoring and biological characteristics. Proceedings of the 2nd Workshop on Jellyfish Blooms in the Mediterranean Sea. UNEP, Athens. Map tech. Rep. Ser. 47: 77–81.
- Christensen, V. & D. Pauly, 1992. ECOPATH II – a software for balancing steady-state ecosystem models and calculating network characteristics. *Ecol. Mod.* 61: 169–185.
- Cram, D. L. & G. A. Visser, 1973. SWA pilchard stock shows first signs of recovery (Summary of results of Phase III of the Cape Cross programme). *S. Afr. Ship. News Fishg. Ind. Rev.* 28: 56–63.
- Denman, K. L. & T. M. Powell, 1984. Effects of physical processes on planktonic ecosystems in the coastal ocean. In Barnes, M. (ed.), *Oceanogr. mar. biol. Ann. Rev.* 22: 125–168.
- Estrada, M. & C. Marrasé, 1987. Phytoplankton biomass and productivity off the Namibian coast. *S. Afr. J. mar. Sci.* 5: 347–356.
- Fearon, J. J., A. J. Boyd & F. H. Schülein, 1992. Views on the biomass and distribution of *Chrysaora hysoscella* (Linné, 1766) and *Aequorea aequorea* (Forskål., 1775) off Namibia, 1982–1989. *Sci. Mar.* 56: 75–85.
- Feigenbaum, D. L. & M. Kelly, 1984. Changes in the lower Chesapeake Bay food chain in the presence of the sea nettle *Chrysaora quinquecirrha* (Scyphomedusae). *mar. Ecol. Prog. Ser.* 19: 39–47.
- Gibbons, M. J., 1994. Diel vertical migration and feeding of *Sagitta friderici* and *Sagitta tasmanica* in the southern Benguela upwelling region, with a comment on the structure of the guild of primary carnivores. *Mar. Ecol. Prog. Ser.* 225–240.
- Gibbons, M. J., N. Gugushe, A. J. Boyd, L. J. Shannon & B. A. Mitchell-Innes, 1999. Changes in the composition of the non-copepod zooplankton assemblage in St Helena Bay (southern Benguela ecosystem) during a six day drogue study. *Mar. Ecol. Prog. Ser.* 180: 111–120.
- Gibbons, M. J. & L. Hutchings, 1996. Zooplankton diversity and community structure around southern Africa, with special attention to the Benguela upwelling system. *S. Afr. J. Sci.* 92: 63–76.
- Graham, W. M., 1994. The physical oceanography and ecology of upwelling shadows. PhD thesis, University of California, Santa Cruz.
- Graham, W. M., 2001. Numerical increases and distributional shifts of *Chrysaora quinquecirrha* (Desor) and *Aurelia aurita* (Linné) (Cnidaria: Scyphozoa) in the northern Gulf of Mexico. *Hydrobiologia* 451 (Dev. Hydrobiol. 155): 97–111.
- Graham W. M., Pagès, F., & W. M. Hamner. 2001. A physical context for gelatinous zooplankton aggregations: a review. *Hydrobiologia* 451 (Dev. Hydrobiol. 155): 199–212.
- Hart, T. J. & R. I. Currie, 1960. The Benguela Current. *Discovery Rep.* 31: 123–298.
- Hernroth, L. & F. Gröndahl, 1983. On the biology of *Aurelia aurita* (L.) 1. Release and growth of *Aurelia aurita* (L.) ephyrae in the Gullmar Fjord, western Sweden, 1982–83. *Ophelia* 22 (2): 189–199.
- Jarre-Teichmann, A., L. J. Shannon, C. L. Moloney & P. A. Wickens, 1998. Comparing trophic flows in the southern Benguela to those in other upwelling ecosystems. *S. Afr. J. mar. Sci.* 19: 391–414.
- King, D. P. F. & M. J. O'Toole, 1973. A preliminary report on the findings of the South West African pelagic egg and larval surveys. SFRI Internal Rep. Cape Cross Progr. Phase III.
- Kramp, P. L., 1961. Synopsis of medusae of the world. *J. mar. biol. Ass. U.K.* 40: 1–469.

- Larson, R. J., 1992. Riding Langmuir circulations and swimming in circles: a novel form of clustering behavior by the scyphomedusae *Linuche unguiculata*. *Mar. Biol.* 112: 229–235.
- Mills, C. E., 2001. Jellyfish blooms: are populations increasing globally in response to changing ocean conditions? *Hydrobiologia* 451 (Dev. Hydrobiol. 155): 55–68.
- Pagès, F., 1991. Ecología sistemática de los Cnidarios planktónicos de la corriente de Benguela (Atlántico Sudoriental). Ph.D. thesis, Univ. Barcelona, 466 pp.
- Pagès, F. & J. M. Gili, 1991. Effects of large scale advective processes on gelatinous zooplankton populations in the northern Benguela ecosystem. *Mar. Ecol. Prog. Ser.* 75: 205–215.
- Purcell, J. E., 1991. Predation by *Aequorea victoria* on other species of potentially competing hydrozoans. *Mar. Ecol. Prog. Ser.* 72: 255–260.
- Purcell, J. E., 1992. Effects of predation by the scyphozoan *Chrysaora quinquecirrha* on zooplankton populations in Chesapeake Bay, U.S.A. *Mar. Ecol. Prog. Ser.* 87: 65–76.
- Purcell, J. E. & M. N. Arai, 2001. Interactions of pelagic cnidarians and ctenophores with fish: a review. *Hydrobiologia* 451 (Dev. Hydrobiol. 155): 27–44.
- Purcell, J. E. & J. H. Cowan Jr, 1995. Predation by the scyphomedusan *Chrysaora quinquecirrha* on *Mnemiopsis leidyi* ctenophores. *Mar. Ecol. Prog. Ser.* 129: 63–70.
- Purcell, J. E. & M. V. Sturdevant, 2001. Prey selection and dietary overlap among zooplanktivorous jellyfish and juvenile fishes in Prince William Sound, Alaska. *Mar. Ecol. Prog. Ser.* 210: 67–83.
- Purcell, J. E., E. D. Brown, K. D. E. Stokesbury, L. H. Haldorson & T. C. Shirley, 2000. Aggregations of the jellyfish *Aurelia labiata*: abundance, distribution, association with age-0 walleye pollock and behaviors promoting aggregation in Prince William Sound, Alaska, U.S.A. *Mar. Ecol. Prog. Ser.* 195: 145–158.
- Russell, F. S., 1970. The Medusae of the British Isles. II. Pelagic Scyphozoa with a Supplement to the First Volume on Hydromedusae. Cambridge University Press, Cambridge: 284 pp.
- Schülein, F., 1974. A review of the SWA pelagic fish stocks in 1973. SFRI Internal Rep.; Cape Cross Progr. Phase IV: 3 pp.
- Schuyler, Q. & B. K. Sullivan, 1997. Light responses and diel migration of the scyphomedusae *Chrysaora quinquecirrha* in mesocosms. *J. Plankton Res.* 19: 1417–1428.
- Shannon, L. J. & A. Jarre-Teichmann, 1999. A model of trophic flows in the northern Benguela upwelling system during the 1980s. *S. Afr. J. mar. Sci.* 21: 349–366.
- Shannon, L. V., 1985. The Benguela ecosystem. 1. Evolution of the Benguela, physical features and processes. In Barnes, M. (ed.), *Oceanography and Marine Biology*. University Press, Aberdeen: 105–182.
- Skeide, R., A. Engås & C.W. West, 1997. Multisampler – a new tool for use in sampling trawls. In Shleinik, V. & M. Zaferman (eds), *Seventh IMR-PINRO Symposium*, Murmansk: 65–76.
- Stander, G. H. & A. H. B. De Decker, 1969. Some physical and biological aspects of an oceanographic anomaly off South West Africa in 1963. *Investl Rep. Div. Sea Fish. S. Africa* 81: 1–46.
- Venter, G. E., 1988. Occurrence of jellyfish on the west coast off South West Africa/Namibia. *Rep. S. Afr. Natn Scient. Progrms* 157: 56–6.