INTRODUCTION

Most medusae are carnivorous and their individual growth rates may be rapid when food is abundant [e.g. (Arai, 1997)]. Many species can also withstand prolonged periods without food [e.g. (Greve, 1972; Costello, 1998)]. These are some of the characteristics of medusae that enable them to be conspicuous components of coastal and oceanic pelagic marine ecosystems.

As global fisheries begin to decline, medusae appear to be coming to the fore (Purcell et al., 1999), and there is evidence that they may be responsible for localized recruitment failures of some fishes [e.g. (Möller, 1984)]. Although the last two decades have seen an increase in research on medusae, our understanding of their role in marine ecosystems is still poor. This lack of knowledge prevents their accurate incorporation into models of ecosystem functioning, such as Ecopath (Christensen and Pauly, 1993).

We present here some basic, but hitherto missing, information on the biometry of two large, widely distributed medusae (Kramp, 1961); *Aequorea aequorea* (Hydrozoa) and *Chrysaora hysoscella* (Scyphozoa). These two species are abundant in the northern Benguela ecosystem (Fearon et al., 1992; Pagès et al., 1992), where they pose a problem to both fisheries and fishery managers (Brierley et al., 2001).

Although the intention is to make these data more generally available, novel information on the biology of the two species, and their parasites is also presented. These data supplement (in part) those presented on *A. aequorea* and *C. hysoscella* in two complimentary papers on hydroacoustic target strength (Brierley et al., 2001) and spatial distribution (Sparks et al., 2001).

**Biometry and size distribution of Chrysaora hysoscella** (Cnidaria, Scyphozoa) and *Aequorea aequorea* (Cnidaria, Hydrozoa) off Namibia with some notes on their parasite *Hyperia medusarum*

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Novel data on the biometry, size distribution and parasites of *Aequorea aequorea* and *Chrysaora hysoscella* are provided from investigations conducted during summer and winter in the northern Benguela ecosystem. The relationship between mass and diameter of *C. hysoscella* did not change on a seasonal basis, and this possibly reflects the aseasonal nature of the food environment. The changes in the size structure of *C. hysoscella* across the shelf and with depth agree with postulated population maintenance strategies in the region. *Aequorea aequorea* was not strongly parasitized, but *C. hysoscella* was subject to occasional parasitism by *Hyperia medusarum*, especially in winter when *C. hysoscella* is thought to reproduce. Parasites were distributed in a typical, negative-binomial manner on their hosts, but load was independent of host size. As medusae increased in diameter so *H. medusarum* tended to move from other tissues to the gonads.
METHOD

The data were collected during summer 1998 and winter 1999 cruises over the Namibian shelf. The winter cruise (August 31–September 6) was conducted on the R/V ‘Dr Fridtjof Nansen’ and sampled at four stations. Stations 1 (22°05’S, 13°27’E, depth 160 m), 2 (21°27’S, 13°38’E, depth 85 m) and 3 (21°50’S, 13°08’E, depth 225 m) were occupied for 24 h each, while ‘Station 4’ was an offshore–inshore transect at 22°00’S, from 12°42’E (depth 430 m) to 13°28’E (145 m).

Net samples during winter were taken using two pelagic trawls. Both nets had 12 m diameter circular mouth openings, and the mesh size reduced from 400 to 36 mm. The larger net was a modified Åkrehamn trawl (Valdemarsen et al., 1994), the other was fitted with a multisampler and three cod ends that enabled three separate samples to be obtained from a single trawl deployment (Skjæde et al., 1997). All the trawls were monitored by SCANMAR trawl sensors for vertical opening. Net hauls were typically of 6 min duration at 5 knots.

Samples during summer (February 13–March 10) were collected aboard the R/V ‘Welwitschia’, in the area between 18°23.6’S and 13°38.7’E, and 11°51.1’E and 23°06.5’E. They were performed using an ENGLES 308 mid-water trawl with a 25 mm cod end.

Net samples were analysed immediately on recovery to determine total number and wet mass of C. hysoscella and A. aequorea. Catches were often very large (several tons), and on these occasions random sub-samples were taken in 40 l fish baskets. Total catch was estimated by multiplying mass and number values per basket by the total number of baskets caught. Jellyfish numerical samples were measured individually. The wet weight was measured to the nearest 0.01 kg for both species, using an electronic balance. The diameter of each specimen was measured to the nearest 0.01 cm using a measuring tape. If some measured parts of the animals were broken, the other measurements were nevertheless considered.

The number and distribution of parasites on each measured medusa was recorded. All other fish or cephalopod species caught with the medusea were also determined and weighed.

RESULTS

A total of 66 net hauls were made during the 5 day winter survey, and a total of 34.87 tons of A. aequorea, and 23.05 tons of C. hysoscella, were caught. The other components of the catches (0.31 tons) were principally some Cape horse mackerel (Trachurus trachurus capensis), Myctophidae (Symphysodon botrops), ribbon fish (Trichiurus trichiurus), or squid (Loligo gamae variegata). Only seven trawls were empty.

Few A. aequorea were found inshore (Figure 1a), and those present were mostly distributed in the upper 30 m (mean density in the upper 30 m, 0.09 individuals 100 m–3). Offshore, A. aequorea was abundant throughout the water column (mean density, 31.36 individuals 100 m–3) but bigger biomasses were found close to the surface (the maximum density at 10 m was 193.99 individuals 100 m–3, corresponding to 1 314 kg m–3). In contrast, C. hysoscella was more abundant inshore (mean density at stations 1 and 2, 0.67 individuals 100 m–3), and reached a maximum density of 3.55 individuals 100 m–3 there (Figure 1b). It was a shallow water species, and 84% of the population was distributed between the surface and 30 m. Only a few individuals were found offshore (the biggest catch of the station 3 was only 0.43 individuals 100 m–3), and they were collected in the upper 30 m.

Aequorea aequorea

A total of 2488 A. aequorea were measured during the survey. Owing to its fragile nature, most of the caught specimens were broken in the net, and only the thick central disc of the umbrella could be measured. However, eight individuals were collected without damage, in which the central disc represented 56% (± 9%) of the total umbrella diameter, and was responsible for 44% (± 12%) of the total weight. References hereafter concern the central disc only. The diameter of the disc ranged from 1.5 to 18.0 cm, and the weight ranged from 0.01 to 0.36 kg. Nearly half of the population (46.2%) had a diameter between 7 and 8 cm (Figure 2a), and most weighed between 50 and 70 g (Figure 2a). The relationship between disc diameter and mass followed a power curve (Figure 3a). Neither the size composition of the population, nor the relationship between disc diameter and mass, varied significantly across the shelf, nor with depth. A comparison of these winter data with those collected during summer did not reveal any seasonal changes in the size structure of the population. Some hyperiid amphipods were found on three A. aequorea during winter (there were no summer records). However, as they did not occur deeply in the mesopelagic, it cannot be assumed that they originated from A. aequorea. They may have become attached to the meduse during the trawl.
Chrysaora hysoscella

A total of 870 C. hysoscella were measured. Many of these were damaged, but had at least two morphological variables that could be measured. Fifty per cent of the population were between 20 and 35 cm in diameter, although individuals ranged in size from 8 to 63 cm (Figure 2b). The mass–frequency histogram of the sampled population (Figure 2b) was skewed towards lighter individuals, and only four weighed more than 8 kg. The relationship between diameter and mass took the form of a power curve (Figure 3c). Although the long oral arms were readily broken, the relationship between their length and diameter was linear (Figure 3d). The diameter of the gonads could be determined in most individuals (Figure 5d), and the relationship between gonad size and umbrella diameter was also best described by linear regression (Figure 3e).

The size structure of the C. hysoscella population changed with both depth and distance offshore (Figure 4). Inshore at station 2, where 97% of the catch was C. hysoscella, animals at the surface were significantly smaller ($t$ test $P < 0.05$; average diameter, 24.0 ± 7.8 cm) than they were at depths greater than 30 m (28.8 ± 10.1 cm; Figure 4a). They were also smaller than individuals in the surface waters further offshore at station 3 (35.3 ±

Fig. 1. Box-whisker plots showing the relationship between medusa density (as individuals 100 m$^{-3}$) and bottom depth for (a) Aequorea aequorea and (b) Chrysaora hysoscella.
8.3 cm), although there was no significant change in the size structure of the population with depth there (Figure 4b).

A comparison of the biometric relationships derived during winter, with those collected during summer, revealed some interesting differences. The population of *C. hysoscella* was composed of generally smaller individuals (Figure 2c) \( t \text{-test}, P < 0.1 \). However, the relationship between diameter and mass was not of significantly different slope (Mann-Whitney Rank test, \( P = 0.579 \)) (Figure 3b).

Parasitism by *Hyperia medusarum* of *C. hysoscella* was not uncommon, and of the 870 individuals examined 37.3% had one or more parasites, and some had more than 10 (Figure 5a). There was no apparent relationship between medusa size and parasite load or the incidence of parasitism (Figure 5b), but the maximum number (43) of parasites was observed on a big *C. hysoscella* measuring 52 cm and weighing 6.0 kg. The parasites were concentrated in the gonads and umbrella, although as the medusae increased in size, so the parasites tended to move to the gonads (Figure 5c). Incidence of parasitism did not change with the biomass of *C. hysoscella* found during the survey (Figure 6), but medusae with parasites...
between diameter and weight of *C. hysoscella* and *Velella velella* prove valuable to others [as did, for example, the data on available in the literature, and it is trusted that they will distributed medusae. These data have not hitherto been information on the biometrics of two common, widely We have presented what we hope will be useful baseline DISCUSSION ally inshore. were more commonly found close to the surface, especi-

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**DISCUSSION**

We have presented what we hope will be useful baseline information on the biometrics of two common, widely distributed medusae. These data have not hitherto been available in the literature, and it is trusted that they will prove valuable to others [as did, for example, the data on *Wula cella* (Arai, 1996)].

The absence of any seasonal change in the relationship between diameter and weight of *C. hysoscella* is interesting, given that variations have been observed for *Aequorea aequorea* (Weisse and Gomoiu, 2000). Although these authors sug-
gested that the seasonal differences reflect changes in the food environment, the absence of any clear seasonality in the food environment over the central Namibian shelf (Hutchings et al., 1991) may account for the observed results. The exponent derived from the relationship between diameter and mass for both species of medusae (Figure 3) falls within the range reported for other species [see data in Table II, (Weisse and Gomoiu, 2000)].

Small *A. aequorea* and *C. hysoscella* have been described from small plankton-net surveys as characteristic of inshore and shelf waters, respectively (Pagès, 1992). It has recently been demonstrated that this apparent horizontal segregation is maintained in large individuals too (Sparks et al., 2001), and the latter authors argue that it reflects biolog-

ical and ecological differences between the two groups (Class Hydrozoa, Order Leptomedusae—*A. aequorea*; Class Scyphozoa, Order Semaecostoma—*C. hysoscella*). The data presented here provide a further glimpse into differences between the two medusae.

The biomass of both species was greater in the upper 30 m, inshore for *C. hysoscella* and offshore for *A. aequorea*. Deeper, very few *C. hysoscella* were found, and the biomass of *A. aequorea* was nearly 10 times less than that close to the surface. The shallow distribution could be associated with a lower sampling effort at depth, because nearly 60% of the trawls were performed between the surface and 30 m, and only 17% were performed deeper than 100 m (corresponding to 16 trawls carried out between 112 m and 380 m). Given this sampling bias [approximately equal numbers of samples were collected by day and night], it is difficult to interpret the vertical distribution of the popu-

lation, although previous studies have indicated that both species are primarily epipelagic. Having said that, species of *Aequorea* are known to extend to 2000 m depth (Kemp, 1959). *Chrysaora quinquesppula* has been shown to adjust its vertical position in the water column in response to light (Schuyler and Sullivan, 1997), and there is some evidence to indicate that *C. hysoscella* may display diel vertical migration in local waters (Pagès and Gili, 1992; Brierley et al., 2001; Sparks et al., 2001). *Aequorea aequorea* appears also to adjust its occupational depth in response to changes in sea surface temperature (Sparks and Gibbons, unpublished data) and it has been shown to perform some vertical migrations in the Benguela system in the upper 200 m (Pagès and Gili, 1992). Although the depth ranges observed here are similar to those reported previously, the preference for near surface waters is likely to reflect a com-

promise between the need to maintain populations on the shelf [see below], and the vertical distribution of food.

The size structure of *A. aequorea* populations remained more or less constant irrespective of vertical or horizontal distribution. Not so *C. hysoscella* which showed a signifi-
cant increase in size both with increasing depth and dis-
tance offshore, and bigger, more mature individuals were found offshore. This cross-shelf size distribution has been previously noted (Fearon et al., 1992). These authors postu-
lated that the ephyrae released by benthic scyphistomae in the north are carried south by the inshore undercurr-
ent, where they mature and then move offshore before being transported northward again in the shelf-edge jet.

While it is tempting to try and determine growth rates of *C. hysoscella* using the seasonal data on the size structure of the population, differences in the sampling area effec-

tively prevent this. However, it appears that, unlike *C. quinquesppula* in the Chesapeake Bay area (Cargo and Schultz, 1966), reproduction of *C. hysoscella* off Namibia
may be centred on winter. It may be influenced by the upwellings, stronger in summer, which bring cold water close to the coasts (Shannon, 1985).

Hyperiid amphipods have long been known to have an intimate relationship with gelatinous zooplankton (Strøm, 1762—in Harbison et al., 1977), and the parasitic nature of the association has been studied by Laval (Laval, 1980). Members of the genus *Hyperia* are primarily parasites of medusae, but also of ctenophores and salps (Thurston, 1977; Laval, 1980). They may behave facultatively as parasites when adults, but they are obligate parasites as juveniles. Our data on the parasites of *C. hysoscella* are amongst the first reported for the southeast Atlantic, and represent the first accounts for *Hyperia medusarum*.

The relationship between parasite load and frequency described a negative binomial curve (Figure 5a), which is
characteristic of many parasite–host relationships (Begon et al. 1990). The absence of a relationship between the size of *C. hysoscella* and parasite load (Figure 5b) probably reflects both the bet-hedging strategy of the parasite, and the seasonality of the host. Following an initial, chance encounter between parasite and host, individual female amphipods are thought to limit the number of young deposited per medusa (Laval, 1980). The parasites seem able to detect the presence of other parasites, and may avoid depositing young on an infected host. The numbers of free-living individuals may also be limited.

The incidence of parasitism is tied to seasonality in the host (Laval, 1971). In the North Sea, for example, amphipods (*Hyperia galba*) and medusae (*Chrysaora hysoscella*) are absent during winter. The incidence of parasitism increases with the occurrence of the medusae and approaches 100% in late summer and autumn, when the medusae are sexually mature, the incidence of parasitism approaches 100% (Dittrich, 1988). Here, the incidence of parasitism was low in summer (4%), whereas in winter it was ~38%, suggesting that sexual reproduction of *C. hysoscella* may occur during this period, which is in accordance with their generally larger size in winter. The data presented here also suggest that amphipods change their distribution on the host with increasing host size, and there was a tendency for individuals to move from non-gonadal tissue to the gonads as the host increased in size. Previous observations have shown that amphipods can be distributed in any of the natural cavities of the host tissue, or be attached to the surface. Adult *Hyperia* may eat prey caught by medusae (which may also account for the incidence of parasitism on the oral arms) (Laval, 1971). However, as also noticed here, it has been suggested that the host’s gonads are the preferred food of adults (Metz, 1987). The carbon and protein content of the gonads is greatly than that of any other tissues (Arai, 1997), and it might therefore be expected that individuals would use these stores in preparation for growth, egg production and protection. These conclusions cannot be supported here because of the absence of data on the sex and size of the hydroids.

The low incidence of parasitism in *A. aequorea* may be an artefact of the data, because most of the collected material was damaged. Appropriate sampling should be performed so that conclusions can be drawn for this species.

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