Acoustic observations of jellyfish in the Namibian Benguela

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ABSTRACT: Multi-frequency acoustic data (18, 38 and 120 kHz) were collected in conjunction with pelagic trawl sampling for gelatinous macrozooplankton during a cruise to the Namibian Benguela in September 1999. Sampling focused specifically on the scyphozoan *Chrysaora hysoscella* and the hydrozoan *Aequorea aequorea*, both of which occur in large numbers, are probably of major ecological importance, and physically hamper pelagic fishing and diamond extraction activities. *C. hysoscella* was detected predominantly at an inshore station and *A. aequorea* was found in greatest abundance further offshore in deeper water. Echo-sounder observations were linked directly to net catches, and relationships between catch density (number of individuals m^{-3}) and nautical area scattering coefficients (s_A) at each frequency were determined for both species in order to estimate target strength (TS) using the comparison method. TS for *C. hysoscella* (mean umbrella diameter 26.8 cm) was –51.5 dB at 18 kHz, –46.6 dB at 38 kHz and –50.1 dB at 120 kHz; for *A. aequorea* (mean central umbrella diameter 7.4 cm) TS was –68.1 dB at 18 kHz, –66.3 dB at 38 kHz and –68.5 dB at 120 kHz. These TS values compared favourably with previously published estimates for related species. Jellyfish were caught at high numerical densities (maxima 3 *C. hysoscella* per 100 m^3, 168 *A. aequorea* per 100 m^3). These high densities, combined with the not unsubstantial TS at frequencies used for fisheries surveys, imply that jellyfish could potentially bias acoustic estimates of fish abundance. We suggest a simple multifrequency approach that could be used to discriminate between echoes from jellyfish and some commercially important pelagic fish in the northern Benguela ecosystem.

KEY WORDS: Acoustics · *Chrysaora hysoscella* · *Aequorea aequorea* · Multi-frequency · Target strength · Benguela · Jellyfish · Namibia

INTRODUCTION

The jellyfish *Chrysaora hysoscella* (class Scyphozoa) and *Aequorea aequorea* (class Hydrozoa) are abundant in Namibian waters. There is some evidence to

suggest that prior to the 1970s this was not the case (e.g. Hart & Currie 1960, Stander & de Decker 1969), and it is possible therefore that these species have become established as a major component of the northern Benguela ecosystem over the course of just 2 or 3 decades (Fearon et al. 1991). Rapid increases in abundance (blooms) of gelatinous carnivores (including medusae, siphonophores and ctenophores) have

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been reported in recent years from numerous marine ecosystems worldwide (e.g. Mills 1995). The increase in jellyfish abundance in the northern Benguela appears to have coincided with a period of declining pelagic fish catches there (Shannon et al. 1992, FAO 1995), and it has been suggested that these phenomena are directly linked. Although the diets of *C. hysoscella* and *A. aequorea* are not well described, related species are known to prey upon fish eggs and larvae (e.g. Purcell et al. 1987, 1994, Purcell 1989); jellyfish also consume other zooplankton that are themselves important sources of food for fish (e.g. Purcell 1992, Suchman & Sullivan 1998). Introduction of the ctenophore *Mnemiopsis leidyi* to the Black Sea has been implicated in the crash of fish stocks there (Travis 1993), and the pattern of increasing jellyfish abundance following finfish decline is becoming well established (Purcell et al. 1999). In addition to their potential predatory and competitive impacts on fish abundance, jellyfish hamper fishing activities off Namibia physically by clogging and subsequently bursting trawl nets. Jellyfish also cause localised problems to the inshore diamond mining industry because they can block the suction devices used to mine marine alluvial sediments.

Despite the probable ecological importance of jellyfish in the northern Benguela ecosystem, and the economic consequences that their large numbers bring, little is known of the biology or population dynamics of *Chrysaora hysoscella* or *Aequorea aequorea*, or indeed of gelatinous zooplankton there generally (Gibbons et al. 1992). Some information on the distribution and abundance of *C. hysoscella* and *A. aequorea* is available from Bongo net surveys (Fearon et al. 1991, Pagès 1991), but these nets were small (57 cm mouth opening) and are unlikely to have provided unbiased data, particularly for adult *C. hysoscella* that attain umbrella diameters exceeding 50 cm. A knowledge of patterns of species distribution and abundance are amongst the most basic requirements for understanding population biology processes, and will be vital for developing hypotheses to explain the behaviour of *C. hysoscella* and *A. aequorea* populations off Namibia.

Acoustic techniques are used commonly for studies of distribution and abundance of fish (e.g. MacLennan & Simmonds 1992) and zooplankton (e.g. Brierley et al. 1997), enabling large areas of ocean to be surveyed non-invasively in relatively short periods of time. Acoustic measurements of caged specimens of the common jellyfish *Aurelia aurita* (Mutlu 1996) and laboratory-held gelatinous zooplankters *Aequorea victoria* and *Pleurobrachia bachei* (Monger et al. 1998) have shown that jellyfish can be detected acoustically, and fishery-acoustic survey techniques may therefore be applicable for these animals too. Jellyfish have also been detected acoustically near the sea floor during

seismic surveys (L. Ricketts, de Beers Marine, pers. comm. 2000). To our knowledge though, there are very few published studies on the use of acoustics at sea to study jellyfish (but see Toyokawa et al. 1997 and references therein, and Purcell et al. 2000), and those studies that are available are predominantly qualitative. The high abundances of *Aequorea aequorea* and *Chrysaora hysoscella* along the Namibian coast provide excellent opportunities for studying jellyfish at sea, as well as a strong motivation for describing their acoustic characteristics: knowledge of mesoscale distribution and abundance variation, which acoustic surveys may be able to provide, would be of great value to a number of parties operating in Namibian waters.

The study reported here was instigated with the general aim of assessing the applicability of acoustic survey techniques at sea for quantitative studies of jellyfish. Specifically our objectives were: (1) to determine the target strengths (TS) of *Chrysaora hysoscella* and *Aequorea aequorea* at frequencies used on fisheries surveys — TS is required to convert echo intensity to animal numerical density; (2) to obtain multi-frequency acoustic data from single-species aggregations of *C. hysoscella* and *A. aequorea* that may enable these species to be both identified (in a similar manner to techniques that have previously been developed for crustacean zooplankton [Brierley et al. 1998] and fish [Simmonds et al. 1996]) and distinguished acoustically from commercially important fish; and (3) to describe the off/inshore distribution of these jellyfish species.

MATERIALS AND METHODS

Survey details. The jellyfish survey was conducted from the FRV 'Dr Fridtjof Nansen' between August 31 and September 6, 1999. The cruise was a component of the Benguela Environment Fisheries Interaction and Training (Benefit) Programme, which is a regional partnership between Namibia, Angola and South Africa focused on fisheries and marine resources of the Benguela Current ecosystem off southwest Africa (see www.benefit.org.na).

The ship sailed from Walvis Bay and, after initial netting trials, occupied an inshore station for a 24 h period between September 2 and 3. This station, at 21° 27′ S, 13° 38′ E, had a water depth of 85 m. An offshore station, at 21° 59′ S, 13° 08′ E, was occupied for a similar period between September 4 and 5. Water depth there was 225 m. Finally an off/inshore transect was run during daylight on September 5 along 22° S between 12° 42′ E (water depth 430 m) and 13° 47′ E (102 m). Net samples were taken along this transect at intervals corresponding to approximately 50 m reductions in bottom depth. Station positions are shown in Fig. 1.
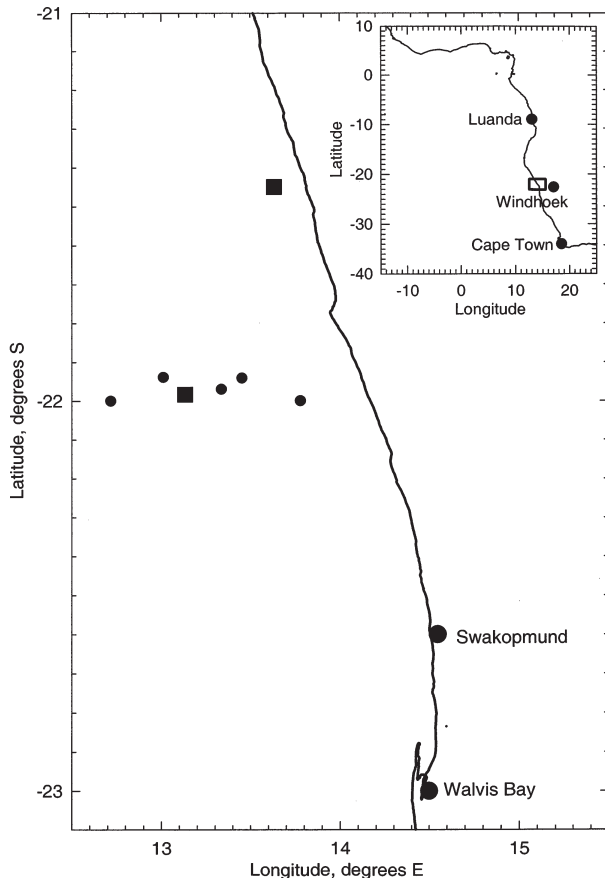
Fig. 1. Map showing 24 h sampling stations (■) and CTD/trawling stations along the transect at 22° S (●) off the Namibian coast

Acoustic sampling. A Simrad EK500 echo-sounder operating 18, 38 and 120 kHz split-beam transducers was run continuously throughout the cruise. The 38 and 120 kHz transducers were mounted on a drop keel at a depth of 8 m, and the 18 kHz transducer was mounted on the ship's hull at 5.5 m. All 3 echo-sounder frequencies were calibrated using standard target spheres on September 12, 1999, at Sandy Point, South Africa. Echo-sounder settings and calibration parameters are given in Table 1.

Acoustic data were logged ping-by-ping over an ethernet to PC using SonarData Echolog_EK software. Ping repetition rate varied with water depth, but was of the order of 1 ping s^{-1}.

Trawl sampling. Net samples were taken with 4-panel pelagic trawls equipped with Scanmar acoustic transponders that provided information on head-rope depth. Two nets were used which, although of different overall sizes, were of the same design (modified Åkrehamn trawl, Valdemarsen & Misund 1994) and were identical from the belly-opening backwards, both having 12 m diameter circular mouth openings (mesh size reducing from 400 to 36 mm): for jellyfish, which will not exhibit a herding response to the net extensions (mesh sizes from 1.6 to 3.2 m), we believe that both nets had the same effective fishing size and efficiency. The smaller net was fitted with a multisampler (Skeide et al. 1997) and 3 cod ends that enabled 3 separate samples to be obtained from a single trawl deployment. The trawl warp for the large net was equipped with balloon floats that kept the net near-surface (effective fishing depth between 19 and 31 m). The smaller net was fished throughout the water column and was most often used to collect samples at 3 discrete depths per deployment. Net hauls were typically conducted at 3 knots and were of 5 min duration (extending approximately 450 m horizontally), except on occasions when very dense concentrations of jellyfish were evident in surface waters and deployments were cut short.

Hydrographic sampling. Casts were made to near-bottom with a Seabird SBE911+ CTD at both of the 24 h sampling stations and at each of the sampling sites on the off/inshore transect along 22° S. Temperature and salinity data were de-spiked and used to derive density (sigma 0). Oxygen concentration was also recorded, although these data can only be considered in relative terms since the water samples needed to calibrate the sensor were not taken.

Catch analysis. Net samples were analysed immediately after the net was recovered to determine total number and wet mass of *Chrysaora hysoscella*, *Aequorea aequorea* and all other fish and cephalopod

Table 1. Echo-sounder settings. TS: target strength; SV: volume backscattering strength; Cu: copper; WC: tungsten carbide

	Frequency (kHz)		
	18	38	120
Transducer type	ES18-11	ES38B	ES120-7
Pulse duration (ms) (Simrad descriptor)	0.7 (short)	1 (medium)	1 (long)
Bandwidth (kHz) (Simrad descriptor)	1.8 (wide)	3.8 (wide)	1.2 (narrow)
Calibration sphere	60 mm Cu	60 mm Cu	38.1 mm WC
Calibrated TS gain (dB) (value used on survey)	21.60 (21.50)	27.65 (27.65)	26.17 (25.62)
Calibrated SV gain (dB) (value used on survey)	21.69 (21.70)	27.45 (27.45)	26.01 (25.62)

species. Catches were often very large (several tonnes), and on these occasions random subsamples 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 density was estimated by dividing the total number of each species in the catch by the volume of water sampled (= $36\pi \times$ horizontal extent of trawl; trawl extent calculated from positions of net shooting and hauling as recorded in the ship's log). Umbrella diameter and wet mass for all jellyfish, or a random sample of 50 individuals of each species, whichever was the lesser, were measured. *C. hysoscella* diameter was measured to the nearest cm, and *A. aequorea* to the nearest 0.5 cm; the wet masses of both species were recorded to the nearest 0.01 kg. Measures of wet mass and total animal volume were made for individual specimens of both jellyfish species so that their body tissue densities could be determined.

Acoustic analysis. Acoustic data (pings) were time-stamped on collection. Those data corresponding to each trawl sample were identified using net-depth, wire-out and simple trigonometry to replot net trajectories over echograms. For example, when fishing the large net near-surface, 130 m of wire were typically payed out which, at a towing speed of 3 knots, equated to a time offset of 84 s between the acoustic and net samples: on a haul to 150 m depth, 450 m of wire were required and this resulted in a 292 s offset between echo-sounder and net.

Acoustic data corresponding to the section of the water column sampled by the net (typically 12 m deep by 450 m horizontally) were integrated using SonarData Echoview software to determine the nautical area scattering coefficients, s_A (units = m^2 nautical mile^{-2}, terminology after MacLennan & Fernandes 1999), for each of the 3 frequencies. The subsequent analysis then involved 4 stages: First, for net samples where *Chrysaora hysoscella* contributed >95% by wet mass to the total catch, and where no fish were caught, s_A was plotted against the *C. hysoscella* numerical density (individuals m^{-3}) determined from the net sample in order to investigate relationships between jellyfish numerical density and echo intensity. Linear regression analysis was used to describe and test the significance of these relationships. This approach of linking echo intensity to a net or other independent estimate of species density has been used widely (e.g. Misund & Beltestad 1996, Gal et al. 1999) and is often referred to as the comparison method (MacLennan & Simmonds 1992). Second, s_A values for trawls where *Aequorea aequorea* contributed >80% by wet mass to the total catch (catches of pure *A. aequorea* were rare), and where the remainder of the catch was predominantly *C. hysoscella* and no fish were caught, were corrected for *C.*

hysoscella numerical density using the regression equations from Stage 1. Corrected s_A values were then plotted against *A. aequorea* numerical density to obtain density/echo intensity relationships for this species. Third, TS for an individual was calculated for both species at each of the 3 frequencies as follows: mean acoustic backscattering cross section $<\sigma_{bs}>$ (m^2) was determined using the equation

$$\rho_v \; = \; \frac{s_A}{1852^2 \, <\sigma_{bs}> \, \Delta z} \qquad (1; \text{ see Ona 1999})$$

where ρ_v (volume density, individuals m^{-3}) and s_A are means as determined from the species- and frequency-specific regression equations, and Δz is the depth over which the acoustic data were integrated (12 m in this case, the effective opening of the net). $<\sigma_{bs}>$ was then expressed as TS in decibels (dB) from

$$\text{TS} \; = \; 10\log_{10}\frac{<\sigma_{bs}>}{4\pi} \qquad (2)$$

Finally, for each species, TS values determined as above for appropriate individual trawls were plotted against $\log_{10}$ mean umbrella diameter for jellyfish in those trawls to investigate TS/size relationships.

RESULTS

A total of 66 net hauls were made during the 5 d survey. Of these, 8 burst under the strain of excessive catches of jellyfish and had to be excluded from analyses because they could not be considered to be quantitative. An additional 2 hauls had to be discarded because either the trawl warp broke or the multisampler acoustic release failed. 14 trawl samples were dominated by *Aequorea aequorea* (>80% wet mass) and 11 contained >95% wet mass *Chrysaora hysoscella*. The remaining hauls could not be used for the purpose of comparison with acoustic data because the catch was either too close to a 1:1 mix of *A. aequorea/ C. hysoscella* to allow backscatter to be attributed solely to one or other species, or was contaminated with fish (including hake, horse mackerel and myctophids) or cephalopods.

From those net samples that were subsequently used for comparison with acoustic data, the mean umbrella diameters of *Chrysaora hysoscella* and *Aequorea aequorea* were 26.8 and 7.4 cm respectively. For *A. aequorea* this diameter refers to the thick central disk of the umbrella. Size-frequency distributions for both species are shown in Fig. 2. *A. aequorea* has a very fragile umbrella margin which was missing or damaged in the majority of individuals we recovered from the net. Eight intact jellyfish were obtained during this study, from which we have estimated that the central
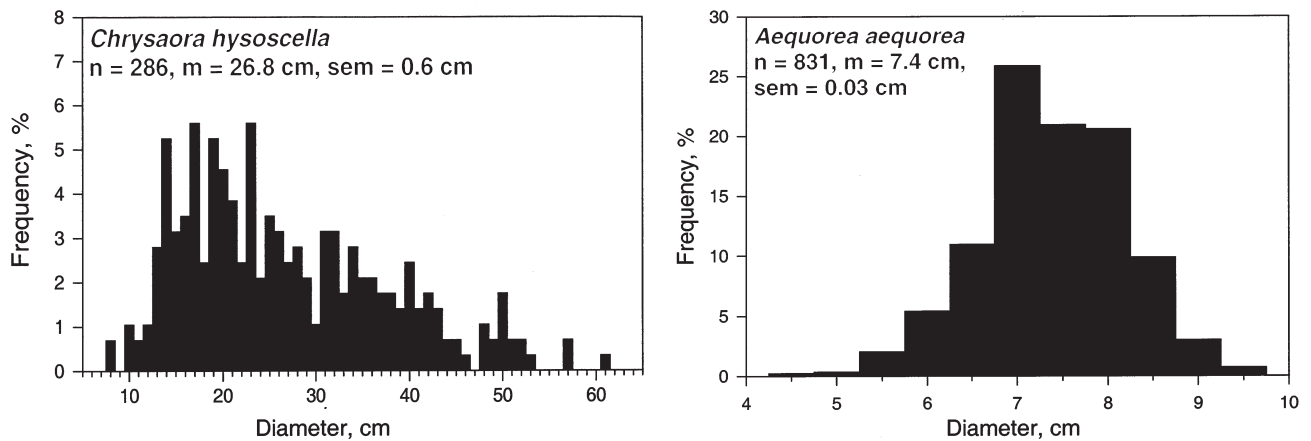
Fig. 2. *Chrysaora hysoscella* and *Aequorea aequorea*. Umbrella diameter frequency distributions for jellyfish from net samples used for comparison with acoustic data (n = sample size, m = mean, sem = standard error of the mean). Diameters for *A. aequorea* are for the central umbrella disk

disk contributes 56 % (±9 %) to total diameter and 44 % (±12 %) to total wet mass. Mean wet mass was 1.15 kg for *C. hysoscella* and 0.06 kg for *A. aequorea*. Animal tissue density was 0.996 kg l^{-1} for *C. hysoscella* and 1.014 kg l^{-1} for *A. aequorea*, although it is not possible for us to conclude whether these values differ significantly.

In broad terms, *Chrysaora hysoscella* was most common at the inshore station, whereas *Aequorea aequorea* was found in greater concentrations further offshore (see Sparks et al. 2000 for more details). The inshore site was dominated by the presence of a persistent scattering layer of about 25 m vertical extent (Figs. 3 & 4A). The layer undulated, but was never
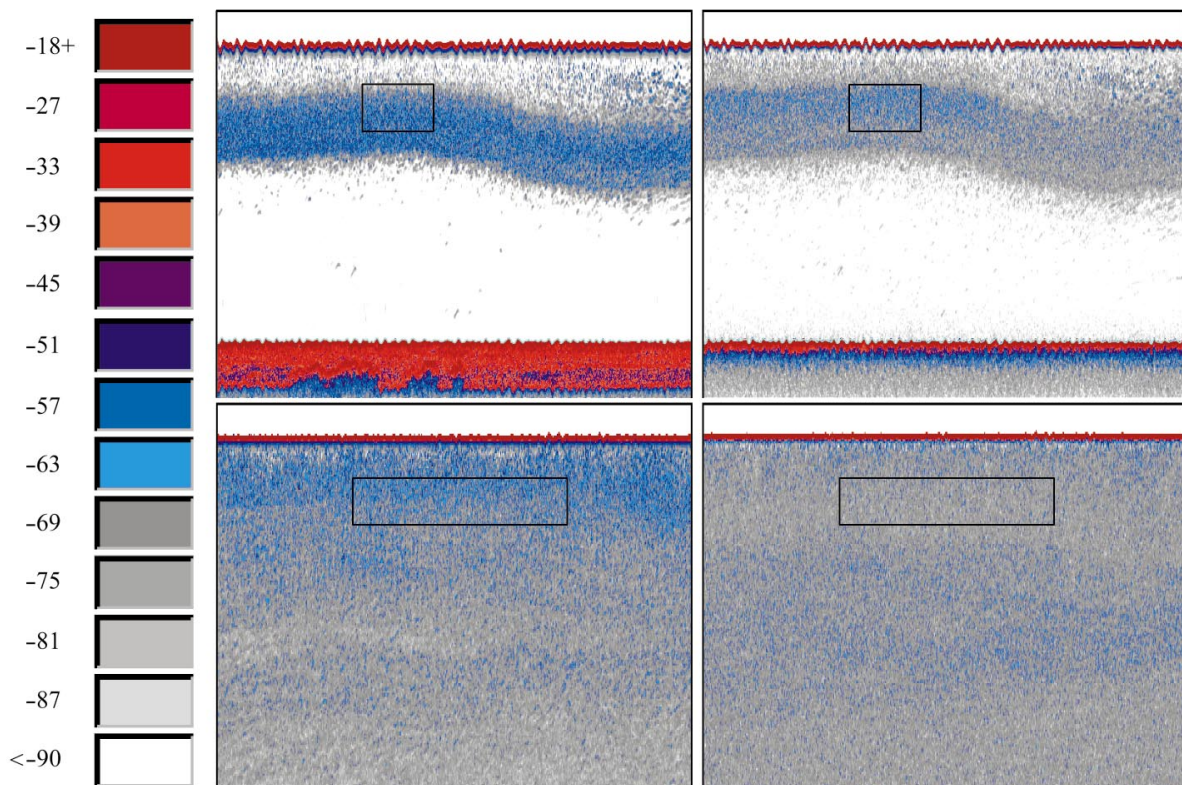

Fig. 3. *Chrysaora hysoscella* (upper panels) and *Aequorea aequorea* (lower panels). Typical daytime 38 kHz (left panels) and 120 kHz (right panels) echograms showing the distinct scattering layer due to *C. hysoscella* and the featureless appearance of *A. aequorea*. Echograms extend 100 m vertically and approximately 1.4 km horizontally; sea bed is visible in the upper panels at about 80 m; display threshold is −90 dB (white), and colour scale (left-hand bar) is in 6 dB steps. Boxes show net sample regions from which pure catches of jellyfish (650 kg *C. hysoscella*, 5340 kg *A. aequorea*) were made. Dense horizontal bands at about 8 m on both echograms are non-biological; they are due to physical transducer effects
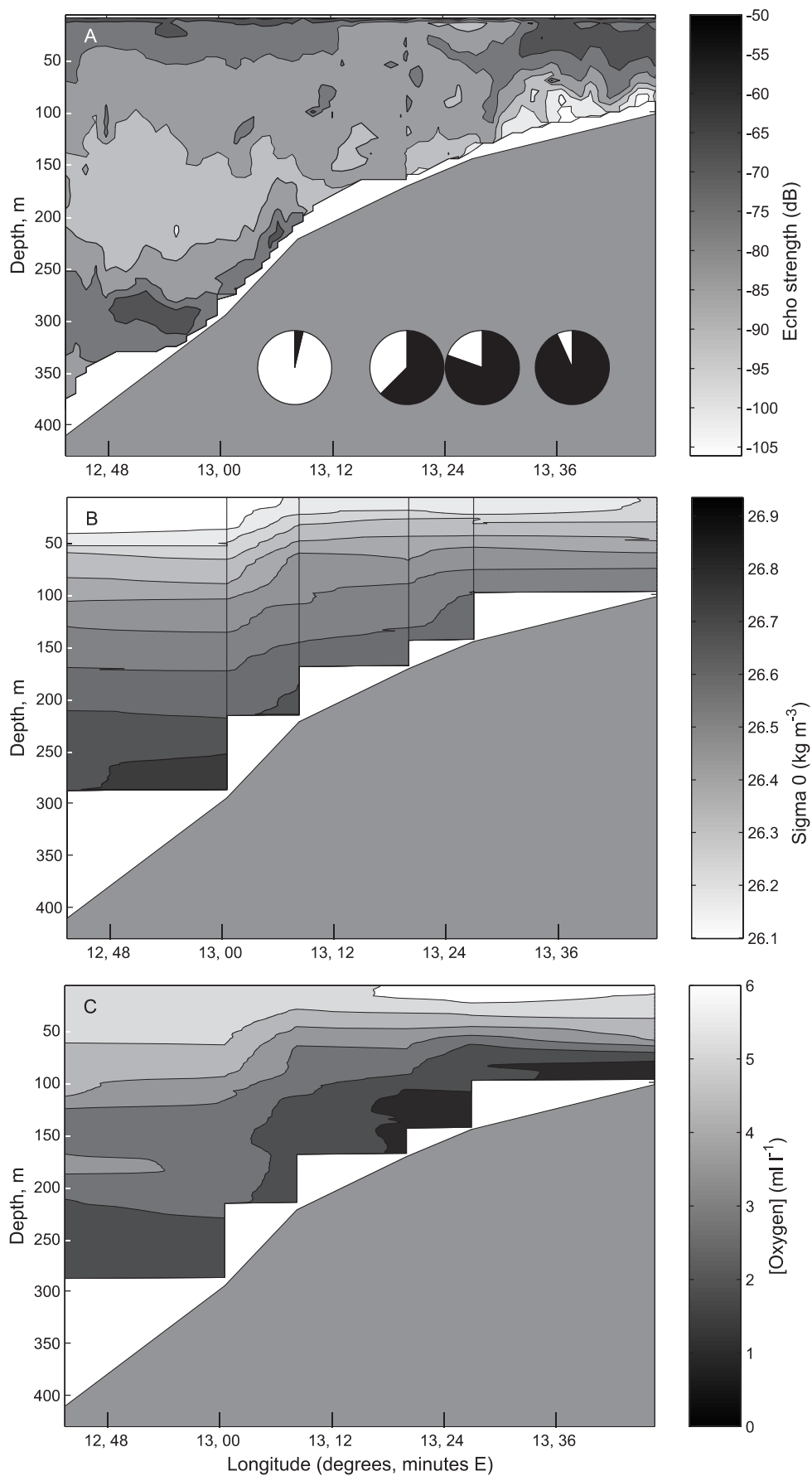
Fig. 4. Off/inshore transect along 22° S. (A) 38 kHz echogram integrated in 5 m × 1 nautical mile intervals showing the prominent scattering layer inshore (top right); inset are pie charts showing the relative proportion (by wet mass) of *Chrysaora hysoscella* (black) and *Aequorea aequorea* (white) in net catches where jellyfish catch rate >100 kg min^{-1} (no such catches were made west of 13° 7′ E). (B) Seawater density (sigma 0, vertical lines and *y*-axes mark the positions of CTD casts). (C) Dissolved oxygen concentration (relative)

observed approaching closer than around 15 m to the surface in daylight. At night the layer became slightly more diffuse, extending its upper boundary towards the surface, presumably as some of the scatterers within it migrated upwards, while the lower boundary remained distinct. *C. hysoscella* was caught in the layer, but fishing beneath the lower boundary failed to catch anything. At the coarsest level, evidence that this acoustically detectable layer was composed of *C. hysoscella* comes from the fact that the largest s_A values (250 m² nautical mile⁻² at 38 kHz, 121 m² nautical mile⁻² at 120 kHz) corresponded to the largest trawl-determined numerical density (≈3 per 100 m³): these data were from a haul near the surface at night that was cut short because very high densities of jellyfish were visible at the surface and we feared that the net would burst. *A. aequorea* was not caught in association with any particularly obvious echogram feature (Fig. 3), and we are not able to associate a characteristic echo type with this species.

Neither species was caught in large numbers west of 13° 7' E and, with the exception of obvious pelagic and near-bottom fish marks, the echogram was effectively blank in this region. The density (sigma 0) section in Fig. 4B shows a substantial shelf-break front centered on 13° 6' E, the steeply sloping contours being indicative of the strong northward flowing Benguela current (see Longhurst 1998). It would appear, therefore, that the jellyfish species targeted in this study are predominantly restricted to continental shelf waters.

Comparison of s_A with *Chrysaora hysoscella* volume density determined from trawl samples produced positive relationships at 18, 38 and 120 kHz (Fig. 5). Slopes of relationships for *C. hysoscella* at 38 and 120 kHz were significantly different from zero (ANOVA, $p < 0.05$). Regression relationships, probabilities and resulting target strengths are given in Table 2. Positive, significant relationships were apparent between s_A and *Aequorea aequorea* volume density at all 3 frequencies (Table 2). Errors in our estimate of sampled volume due to net distortions away from the idealized circular opening, or from clogging by large catches (see Everson & Miller 1999, Holliday 1999), may have effected our TS estimates. Net clogging, in particular, may have reduced the effective volume filtered, particularly at high jellyfish densities, leading to an underestimate of animal volume density and consequently to an overestimate of TS per individual.

The larger *Chrysaora hysoscella* had a substantially greater mean TS per individual (>16 dB) at all 3 frequencies than the smaller species, *Aequorea aequorea*. Once scaled to TS kg⁻¹ (by mean mass per individual), however, the differences between species were less marked, ranging from 3.8 dB kg⁻¹ at 18 kHz to 6.9 dB kg⁻¹ at 38 kHz (see Table 2). Although there were significant differences between the distributions of *C. hysoscella* umbrella diameters in some net hauls, further analyses attempting to link TS to mean umbrella diameter failed to establish significant relationships at any frequency for this species. For *A. aequorea*, positive TS/log₁₀ umbrella
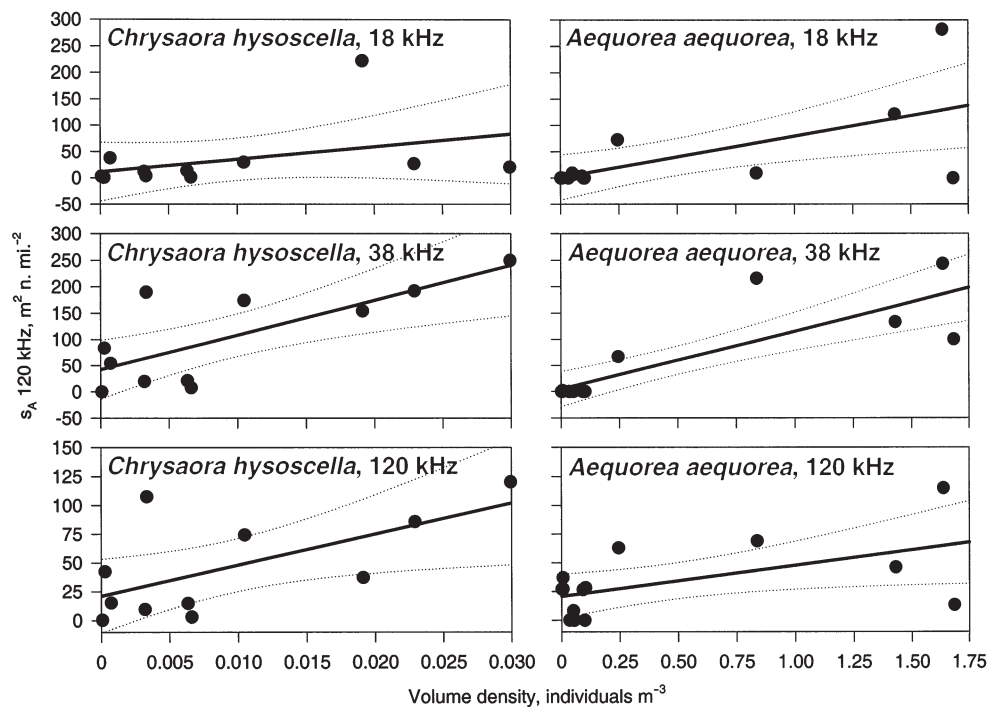

Fig. 5. *Chrysaora hysoscella* and *Aequorea aequorea*. Relationships between nautical area scattering coefficients (s_A) at 18, 38 and 120 kHz and volume density of jellyfish. Continuous lines are regressions, which are bounded by their 95% confidence limits (dashed). Note that *y*-axes are not all at the same scale. n.mi. = nautical mile

Table 2. *Chrysaora hysoscella* and *Aequorea aequorea*. Linear regression relationships and associated r^2 and p (ANOVA, null hypothesis slope = 0) values between nautical area scattering coefficients (s_A, m^2 nautical $mile^{-2}$) at 18, 38 and 120 kHz and volume density (ρ_v, m^{-3}). Mean target strengths (TS, dB) per individual and their 95% confidence intervals (CI) from the regression relationships are shown for both species at each frequency. We are unable to report a lower 95% CI for TS at 18 kHz for either species because the regression equations suggest s_A to be negative (see Fig. 5). Mean target strengths per kg (based on mean TS and mean wet mass per species) are also given

| | Species (mean wet mass) | |
	C. hysoscella (1.15 kg)	*A. aequorea* (0.06 kg)
18 kHz regression	$s_A = 11.8 + 2385\,\rho_v$, r^2 0.15, p 0.25	$s_A = 0.8 + 78.8\,\rho_v$, r^2 0.42, p 0.01
38 kHz regression	$s_A = 44.8 + 6485\,\rho_v$, r^2 0.54, p 0.01	$s_A = 4.7 + 110.7\,\rho_v$, r^2 0.70, p 0.00
120 kHz regression	$s_A = 22.1 + 2658\,\rho_v$, r^2 0.39, p 0.04	$s_A = 20.8 + 27.0\,\rho_v$, r^2 0.30, p 0.04
TS 18 kHz (95% CI)	–51.5 dB (–48.0 dB to – ? dB)	–68.1 dB (–65.0 dB to – ? dB)
TS 38 kHz (95% CI)	–46.6 dB (–45.1 dB to –48.9 dB)	–66.3 dB (–64.5 dB to –69.5 dB)
TS 120 kHz (95% CI)	–50.1 dB (–48.3 dB to –53.3 dB)	–68.5 dB (–66.7 dB to –71.5 dB)
TS kg^{-1} 18 kHz	–52.1 dB	–55.9 dB
TS kg^{-1} 38 kHz	–47.2 dB	–54.1 dB
TS kg^{-1} 120 kHz	–50.7 dB	–56.2 dB

diameter relationships were apparent at all 3 frequencies, and the relationship at 38 kHz was significant (Fig. 6, TS 38 kHz = –329 + 298 $\log_{10}$ umbrella diameter, $r^2 = 0.899$, p = 0.014).

DISCUSSION

Net sample and visual observations made during this survey have shown that the jellyfish *Chrysaora hysoscella* and *Aequorea aequorea* occur in very high numerical densities in the northern Benguela ecosystem off Namibia. Our mean catch densities of 1 and 45 individual *C. hysoscella* and *A. aequorea* per 100 m^3, respectively, in hauls that we have been able to associate directly with acoustic observations (maxima were 3 and 168 per 100 m^3), when viewed in conjunction with published feeding rates for related species (e.g. Purcell 1989, 1992, Purcell et al. 1994), suggest that by weight of numbers alone, these gelatinous macrozooplankton must now play a considerable role in trophic

Fig. 6. *Aequorea aequorea.* Variation of target strength at 38 kHz as a function of umbrella diameter. Continuous line is regression, bounded by 95% confidence limits (dashed)

processes in the northern Benguela. The overall catch maxima during this survey as a whole suggest that the impact is greater still. The possibility that there has been a regime shift in this pelagic ecosystem, with jellyfish proliferating to the detriment of fish (cf. Mills 1995, Purcell et al. 1999), and the further possibility that predation and competition effects may render this paradigm change irreversible, make jellyfish an important group for study.

There are few published TS estimates for jellyfish. Most measurements that have been reported are at or above 120 kHz, and were made on species somewhat smaller than *Chrysaora hysoscella* (e.g. Wiebe et al. 1990, Monger et al. 1998). We are unaware of any previously published 18 kHz TS estimates for jellyfish, and our data must therefore be viewed in isolation. The only 38 kHz data of which we are aware are observations by O. Nakken (cited in Mutlu 1996) on *Aurelia autrans*, where TS was reported to range from –54 dB for an individual 8 cm in diameter to –51.7 dB for a 16 cm specimen. These values are much higher (by about 12 dB) than our observations on similarly sized *Aequorea aequorea* (mean central umbrella diameter 7.5 cm), but only about 3 dB below the lower 95% confidence interval (–48.9 dB) that we determined for *C. hysoscella* TS at 38 kHz (see Table 2). Nakken is also reported to have made measurements at 120 kHz (see Mutlu 1996), finding TS between –54.2 dB (8 cm diameter) and –50.1 dB (16 cm). Nakken's value for the 16 cm individual is equivalent to our mean TS for *C. hysoscella* at 120 kHz, and Fig. 2 shows that the range of *C. hysoscella* diameters we encountered includes 16 cm. Nakken's 8 cm 120 kHz TS is however substantially greater than our estimate at this frequency for *A. aequorea*. *Chrysaora* and *Aurelia* are both members of the order Semaeostomeae (scyphomedusae), whereas *Aequorea* is a member of the order Leptomedusae
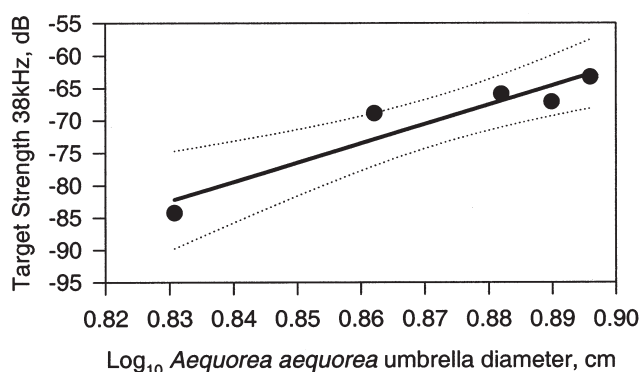
(hydromedusae). The large differences in TS between our observations on *Aequorea* and Nakken's on *Aurelia* could be due in part to differences in their body composition that may be reflected in their more distant taxonomic classification: female *Aurelia* spp. carry clumps of developing larvae, and the gonads can be very dense; scyphomedusae are generally more robust than hydromedusae; the umbrella of scyphomedusae is thicker and firmer and they have long, dense oral arms; the mesoglea of scyphomedusae is composed of living tissue and, finally, hydromedusae have a simple gastric sack, whereas scyphomedusae have convoluted gastric pouches. The carbon content of the 2 groups may also differ (e.g. Larson 1987). Monger et al. (1998) have suggested that the large differences in TS between the gelatinous zooplankton *Aequorea* and *Pleurobrachia* (a ctenophore) were due to differences in sound-scattering properies. Density and sound-speed contrasts, among other things (see Stanton et al. 1996), affect the degree to which objects scatter sound. We were only able to measure density for *C. hysoscella* and *A. aequorea* in the present study: these measurements did suggest differences between species (density was 0.996 kg l^{-1} for *C. hysoscella* and 1.014 kg l^{-1} for *A. aequorea*) but, without replication, are inconclusive.

Mutlu (1996) made measurements of backscatter at 120 and 200 kHz from caged *Aurelia aurita* (umbrella diameter 9.5 to 15.5 cm). Extrapolation from his 120 kHz TS/umbrella diameter relationship gives a TS of −53.6 dB for an individual 27 cm in diameter (the mean for *Chrysaora hysoscella* in this study), which is only just below our lower 95 % confidence interval for *C. hysoscella* TS (−53.3 dB, see Table 2). Extrapolation in the opposite direction to diameter 7.5 cm gives a TS at 120 kHz of −61.7 dB, which is somewhat higher that our estimate of −68.5 dB for *Aequorea aequorea*. Again then, there is closer agreement with our and previously published TS estimates within the order Semaeostomae than without.

Monger et al. (1998) made measurements of *Aequorea victoria* (diameters between 2.6 and 5.8 cm) at 200, 420 and 1000 kHz. They used reduced target strength (RTS),

$$RTS = 10 \log_{10} \frac{<\sigma_{bs}>}{\pi a^2} \qquad (3)$$

(where *a* is the individual's radius) to compare their TS estimates with those made by Mutlu (1996) for larger individuals at lower frequencies. Monger et al. (1998) reported an RTS, averaged over all frequencies and sizes, of −43.3 dB, and stated that their observations were 'in very good agreement' with those of Mutlu (1996) (RTS = −40.7 dB calculated from their Table 1). Averaged in the same way, our RTS value for *A.*

aequorea (assuming a diameter of 7.5 cm) is −44.1 dB, and is −37.0 dB for *C. hysoscella* (diameter 27 cm). We compare published TS values from all species, sizes and frequencies with our own observations by plotting RTS against *ka* (*k* is wavenumber = $2\pi/\lambda$, and *a* is jellyfish radius) (Fig. 7). Our RTS estimates fall within the (albeit large) bounds of previous estimates. The strong dependence of RTS upon *ka* when *ka* is low (Rayleigh scattering), evident from our *A. aequorea* data in Fig. 7, is also noteworthy, since it is in general agreement with both sound-scattering theory (see Medwin & Clay 1998) and specific predictions made by models of sound scattering by *A. victoria* (Monger et al. 1998; see their Fig. 6). The gradient of the regression equation of TS against $\log_{10}$ umbrella diameter upon which this is based (see present Fig. 6) is far steeper than the slope usually expected for fish (see MacLennan & Simmonds 1992). This is probably due in part to the fact that echo-sounder frequencies used for fishery acoustic surveys are usually chosen to be high enough to provoke geometric rather than Rayleigh scattering from the target species.

It is possible that the TS values we have obtained here by the comparison method are greater than the true values. We are unable to discount the possibility that organisms in addition to the jellyfish that were retained in the trawl contributed to detected echo intensities. We were unable to sample zooplankton, for example, in the pelagic trawl, and the smallest organisms we retained were myctophid fish (~ 5 cm). The productive Benguela boundary current ecosystem
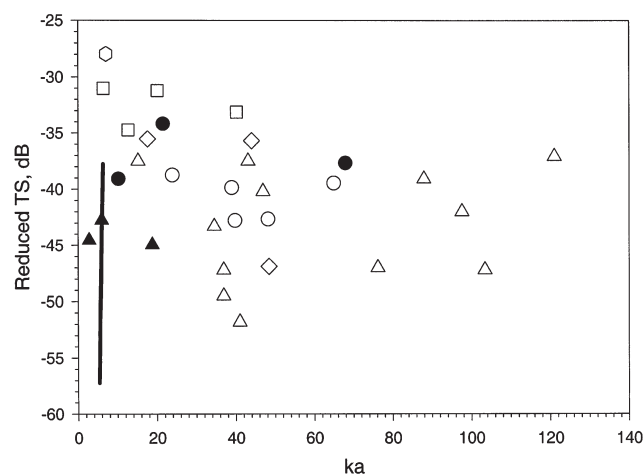

Fig. 7. Summary of reduced target strength (TS) against *ka* for various jellyfish species (*k* is wavenumber = $2\pi/\lambda$, *a* is jellyfish radius): (▲) *Aequorea aequorea* (this study); (●) *Chrysaora hysoscella* (this study); line = *A. aequorea* 38 kHz regression (this study, see Fig. 6); (△) *Aequorea victoria* (Monger et al. 1998); (○) *Aurelia aurita* (Mutlu 1996); (□) *Aurelia autrans* (O. Nakken, cited in Monger et al. 1998); (◇) *Aequorea victoria* (Wiebe et al. 1990); (◯) *Aurelia aurita* (Saito et al. 1990, cited in Toyokawa et al. 1997)

(Baird et al. 1991) supports rich zooplankton communities (e.g. Barange & Stuart 1991, Gibbons & Hutchings 1996), and even small zooplankton can produce intense echoes (see Stanton et al. 1996). The scattering layer we observed may have been due to small zooplankton, and the jellyfish may have been aggregating in the layer because the food supply was elevated there. However, for reasons outlined earlier, we believe that the scattering layer was predominantly due to jellyfish. TS estimates reported by Monger et al. (1998) would not have been subject to this source of error, since their measurements were made in an enclosure containing seawater filtered through 53 μm netting. In addition to possible contamination by free-swimming zooplankton, *Chrysaora hysoscella* was also parasitized by hyperiid amphipods (including *Hyperia galba*, mean infestation level 1.4 parasites per jellyfish) which would also have contributed to σ_{bs} (cf. Trevorrow & Tanaka 1997). We also observed air bubbles inside the gonads and gastric pouch of *C. hysoscella* which were almost certainly introduced during trawling. If these were natural occurrences, however, then these too would have contributed to TS.

Although our TS values may potentially be higher than laboratory-determined values, the fact that our data were collected in the field makes them valuable for consideration of the effect that jellyfish could have on acoustic estimates of fish biomass, because during fish surveys it will be whole water-column values rather that idealized laboratory values that are obtained. Field observations will also include echoes from animals in varying orientations: tank measurements tend to be made on tethered animals held in 1 direction only, but orientation may have considerable effect on TS. Mutlu (1996) has also shown that jellyfish TS changes as umbrella diameter oscillates during swimming. Field observations will be of a 'mean' swimming dilation, which may be different to that adopted by anaesthetized, tank-held individuals. *In situ* TS estimates using multifrequency techniques (Demer et al. 1999) that avoid shortcomings of more basic single-target detection algorithms (see Soule et al. 1995) could provide valuable additional data on the acoustic properties of jellyfish, and offer an obvious avenue for future research.

The high numerical densities and apparently not insubstantial TS that we have observed for *Chrysaora hysoscella* and *Aequorea aequorea* raises the possibility that echoes from these jellyfish may bias acoustic estimates of fish biomass. Indeed, Purcell et al. (2000) have reported that in Prince William Sound nets targeted at acoustic features thought to be fish schools sometimes resulted in large catches of *A. aequorea*. Acoustic surveys are conducted in the Benguela ecosystem to estimate stock sizes of pilchard, horse mack-

erel and anchovies (e.g. Barange et al. 1996). An important stage in the interpretation of acoustic survey data is ensuring that only echoes from the species under investigation are included in estimates of biomass. In the Southern Ocean, for example, acoustic survey techniques are used to estimate sizes of Antarctic krill *Euphausia superba* stocks. Madureira et al. (1993) developed a 2-frequency acoustic classification that allowed echoes from krill to be distinguished from squid/fish and zooplankton. The technique works because these different groups of animals have different relative TS at 38 and 120 kHz and, as a consequence, calculation of $\Delta MVBS_{120\,kHz-38\,kHz}$, the difference in mean volume backscattering strength (S_v, dB re 1 m^{-1}) at 120 and 38 kHz, allows them to be separated: targets where $2\,dB \leq \Delta MVBS_{120\,kHz-38\,kHz} \leq 12\,dB$ are classified as krill. This technique is now used routinely for krill biomass estimation (e.g. Brierley et al. 1997, 1999), and has been extended using an additional frequency (200 kHz) to identify additional zooplankton taxa (Brierley et al. 1998). A technique of this kind could have utility in the Benguela system. Nakken & Olsen (1977) have reported TS estimates for fishes at 120 and 38 kHz, and their data suggest a mean $\Delta MVBS_{120\,kHz-38\,kHz}$ of 3.1 dB for horse mackerel (33 cm long). The $\Delta MVBS_{120\,kHz-38\,kHz}$ for *C. hysoscella* and *A. aequorea* are −3.3 dB (range from 95% CI = 0.6 to −8.2 dB) and −2.2 dB (range = 2.8 to −7.0 dB) respectively: the difference between jellyfish and mackerel offers a potential discriminant function. Although there have been several recent studies on the TS of anchovy and pilchard at 38 kHz, we have been unable to find data at 120 kHz. Barange et al. (1996) have suggested that the closest comparison would be with herring, and Edwards et al. (1984) have reported TS values for mixed herring/sprat aggregations of −49.0 dB at 38 kHz and −51.6 dB at 120 kHz: this yields a $\Delta MVBS_{120\,kHz-38\,kHz}$ of −2.6 dB, which is similar to jellyfish. This simple technique is clearly species- (and probably size-)specific, and does not offer a universal solution for jellyfish/fish discrimination. In the case of *A. aequorea*, where the s_A density relationship was significant, additional discriminatory power could perhaps be brought to bear using 18 kHz data as well (cf. Brierley et al. 1998), but we have been unable to find published TS estimates for these fish species at 18 kHz.

It has not been possible for us to distinguish between *Chrysaora hysoscella* and *Aequorea aequorea* on the basis of relative echo intensities at 120 and 38 kHz alone. Previous studies attempting to use acoustic observations to identify species have found that inclusion of additional information, for example on location in the water column, often improves powers of discrimination (Haralabous & Georgakarakos 1996, Brierley et al. 1998). Consideration of prevailing oceanographic

conditions might also help. Inspection of the density and relative oxygen concentration sections in Fig. 4 in conjunction with the echogram and species-catch distribution reveals that *C. hysoscella* was caught inshore in association with the elevated oxygen levels. The scattering layer is very obvious here. The transition from dominance in catch of *C. hysoscella* to *A. aequorea* occurs around 13° 24′ E, and is coincident with a discontinuity in both oxygen concentration and density. This discontinuity is not as pronounced as the shelf-break front, but nevertheless reveals that the shelf waters are not homogenous. The scattering layer disperses in the vicinity of the oceanographic discontinuity and provides further evidence that the 2 species of jellyfish are differentially distributed. One explanation for this difference might be that *C. hysoscella*, with its greater body size, has a requirement for well-oxygenated waters (but see Breitburg et al. 1999), and is restricted from regions further offshore influenced by the encroaching oxygen minimum that is a feature of the Benguelan upwelling (see Longhurst 1998).

Combinations of acoustic, oceanographic and net sampling data will be needed to fully understand factors influencing the distribution and abundance of *Chrysaora hysoscella* and *Aequorea aequorea* in the northern Benguela current ecosystem. Such combinations will however be of use in Namibian waters, and may serve to aid commercial fishing activities, reducing incidences of net burst, and inform diamond extractors when it is likely that jellyfish may hamper their activities, in addition to revealing more of the ecological dynamics of a group of organisms that are becoming increasingly important in marine ecosystems worldwide.

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