

Pinging down the food web: multi-frequency acoustic discrimination of jellyfish and fish

Christopher P. Lynam, Andrew S. Brierley, and Bjørn E. Axelsen

Jellyfish are gaining increasing prominence in many pelagic marine ecosystems worldwide. It has been argued that jellyfish-dominated communities will be the end-point in ecosystems perturbed by high fishing effort, and that increases in jellyfish abundance could be indicative of, and consequences of, climate-induced changes and/or regime shifts in pelagic ecosystems. Jellyfish are difficult to sample using conventional netting techniques, and data on changes in distribution and abundance are consequently sparse. Recent field observations and modelling studies have however shown that jellyfish can be detected acoustically at frequencies used routinely for fisheries surveys (18, 38, 120 and 200 kHz). Acoustic surveys might therefore provide a means for monitoring jellyfish populations but, prerequisite to this, echoes arising from jellyfish must be distinguishable from echoes returned by other scatterers. This paper presents multi-frequency acoustic data for two jellyfish that are common in the Namibian Benguela; *Chrysaora hysoscella* and *Aequorea aequorea*, and explores how characteristic acoustic signatures of jellyfish may enable these organisms to be discriminated acoustically from pelagic fish including horse mackerel (*Trachurus trachurus capensis*) and pilchard (*Sardinops ocellatus*). The ability to discriminate jellyfish and fish using multi-frequency acoustic data may lead to improved acoustic estimates of pelagic fish biomass (by reducing bias due to jellyfish echoes) and aid ecological investigations of jellyfish.

Keywords: acoustic, Benguela, discrimination, fish, horse mackerel, jellyfish, multifrequency, pilchard.

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Introduction

Interest from the fisheries community in gelatinous zooplankton has grown in recent years due to the increasing disruption caused to fishermen and fish-farmers by jellyfish, and by the realisation that jellyfish can adversely affect fish recruitment (Lynam et al. in review; Mills 2001; Purcell & Arai 2001). The anchovy (*Engraulis encrasicolus*) fishery in the Black Sea was severely depleted during in the 1970s by a combination of fishing, eutrophication, and a subsequent increase in the biomass of the Cnidarians *Rhizostoma pulmo* and *Aurelia aurita*, and finally collapsed after an invasion of the Ctenophore *Mnemiopsis leidyi* in the late 1980s. It is widely believed that the consumption of zooplankton by this gelatinous invader, and the consequent depletion of fish food, was the principal cause of the collapse (Daskalov 2002; Kideys 2002). Medusae also impede fishery activities directly by blocking and bursting trawl nets (Brierley et al. 2001). Climate changes and/or regime shifts may also induce changes in the abundance of medusae (Brodeur et al. 2002; Lynam et al. 2004). Pauly et al. (1998; 2002) suggested that jellyfish may, in fact, be the end point of overexploited marine ecosystems.

Jellyfish have not historically been considered as a source of bias in hydroacoustic estimates of fisheries biomass. However, modelling studies have shown that medusae, despite their delicate bodies, may be strong acoustic scatterers (Monger et al. 1998; Mutlu 1996). Recent observations have shown that backscatter from medusa, salp and ctenophore swarms may be as great as to that from pelagic fish such as sardines and horse mackerel (Brierley et al. 2004; 2001; Colombo et al. 2003). It would be advantageous, therefore, to be able to distinguish jellyfish from fish acoustically. Here, we show that aggregations of *Chrysaora hysoscella* (Scyphozoa) and *Aequorea aequorea* (Hydrozoa) medusae can be distinguished from each other and from schooling fish using multifrequency (18, 38, 120, and 200kHz) acoustic back-scatter. We also compare the distributions of TS for medusae to those of the small pelagic fish (horse mackerel *Trachurus trachurus capensis* and pilchard *Sardinops ocellatus*) and explore the possible degree of misallocation of acoustic backscatter by jellyfish to fish,

which could lead to a possible bias in stock assessment using this method.

Materials and methods

Data collection

Data were collected in August 2003, during a 10-day cruise on the RV "Dr Fridtjof Nansen" that sailed from Walvis Bay, Namibia, to Cape Town, South Africa. Acoustic data were collected simultaneously at 18, 38, 120, and 200 kHz throughout the cruise using continuously-run SIMRAD EK500 echosounders on board the research vessel. The 18, 38 and 200 kHz transducers were all split-beam while the 200kHz transducer was a single-beam. The echosounders were calibrated using standard targets prior to the cruise. Pelagic trawls (typically lasting for 5 min) were undertaken on occasions when jellyfish were observed at the surface and/or when the echograms suggested that medusae were present at depth. Fishing activities essentially followed those described for a previous investigation of jellyfish in Namibian waters from the RV "Dr Fridtjof Nansen" (Brierley et al. 2004; Brierley et al. 2001). Species composition, and size and mass distributions of all fish and jellyfish species, were determined for all trawls.

Acoustic data manipulations

All processing was conducted using SonarData Echoview Vol. 3.1. Acoustic data were noise corrected by subtraction of generated time-varied-gain echograms from the raw data (Watkins & Brierley 1996). The noise corrected data were then spatially matched across frequencies in order to compensate for the relative depths of the transducers (Korneliussen 2002). Since each transducer had a unique beam angle, differences in S_v , due merely to the differing volume sampled, were anticipated. To compensate for this difference, S_v were standardised relative to the narrowest beam (the 38 kHz) (Table 1). The volume-standardised data were then smoothed vertically and horizontally by convolution to reduce the mismatching of depth-binned data due to resolution differences between beams (Korneliussen 2002); each bin value was weighted by its surrounding values using a 5x5

gaussian convolution matrix centred on the bin to be smoothed (Table 2). Finally, pairwise linear difference S_v echograms (dB) were constructed.

Filter construction

S_v data for *A. aequorea* were exported from areas where trawling indicated 100% jellyfish by mass, with $\geq 97\%$ of *A. aequorea* and the remainder *C. hysoscella*. For *C. hysoscella*, data were exported from areas where the proportion of jellyfish by mass in the netting was greater than 89% and that of fish was no greater than 10%. Horse mackerel were found in dense schools and, for this species we exported school-only S_v data. Non-school data was excluded by using a 'minimum data threshold' of -70 dB in Echoview. This optimal threshold was chosen through inspection of the echograms. In contrast, pilchard were found mixed with *A. aequorea*, and located on the echogram within a dense continuous layer where schools could not be distinguished by a minimum data threshold alone. However, *A. aequorea* data could be filtered out using the newly created filter as follows.

Histograms of multifrequency S_v -difference data were inspected for each species. If any combination deviated dramatically from normality (i.e. appeared flat or multimodal) then all S_v for that area of the echogram were considered contaminated by another species and were thus rejected. Selected data were then pooled by species and the means and standard deviations were calculated for each distribution of S_v -difference and a weighted 95% confidence interval was then formulated as mean $\pm 1.96 \times (\text{standard deviation} / \text{square root of the number of trawl samples})$. These intervals were then used to create bitmasks in Echoview to filter the acoustic data, so that only echoes with frequency differences satisfying each requirement associated with a particular fish or jellyfish species were allocated to that species. The resulting filtered echograms were then inspected relative to trawl catches to evaluate the success of the filters. The filter for *A. aequorea* could then be used to remove backscatter due to *A. aequorea* from the pilchard signal in the mixed pilchard/*A. aequorea* area; we first filtered the S_v data for all data that was not due to *A. aequorea* then attributed the

rest to pilchard and created a filter for this species as described above.

Single Targets

Single target detections at each frequency were exported from the horse mackerel schools and the selected trawled areas of *A. aequorea*, *C. hysoscella* and pilchard (6, 2, and 1 trawls respectively). These TS data were analysed using Matlab, in order to increase the probability of accurate allocation to species, and targets were only attributed to the appropriate species if they matched by depth and time with the filtered S_v . TS data were additionally screened to select data points detected simultaneously at all frequencies (Demer et al. 1999). For pilchard, no single targets detections were found in the trawled area that was used for S_v data export. Therefore the least contaminated of the remaining high-biomass pilchard areas was chosen. The trawl in this region contained 68% pilchard, 31% *A. aequorea* and 1% pelagic gobies (*S. bibrabatus*) by mass.

Results

Trawl nettings

A. aequorea was found in dense swarms more often than *C. hysoscella* was and net samples purely of *A. aequorea* were obtained (100% by mass). Pure horse mackerel samples were also found. The pilchard (*Sardinops ocellatus*) was also caught during the survey. However, the only high catch (100%) was at the surface where the echo return is masked by the transmit. Of the ten trawls that contained pilchard, the only other that caught pilchard in high biomass but did not also contain other fish (e.g. Gobies *Sufflogobius bibrabatus*), was split by mass between pilchard 55% and *A. aequorea* 45%.

Backscatter filters

Six trawls were found to contain $\geq 97\%$ *A. aequorea* by mass and no fish, the S_v data associated with these 6 trawls were pooled and histograms were constructed (Figure 1) and the 95% confidence interval, scaled by the square root of 6, was used to create the S_v -filter (Table 2).

Four trawls collected $\geq 89\%$ by mass of *C. hysoscella* with the remaining mass comprising *A. aequorea* and horse

mackerel. By inspection, 2 of the S_v -difference histograms showed signs of contamination by a non target species (i.e. multimodal or broad non-normal distributions) and these data was not used for the construction of the filter.

Two trawls approximately 1 km apart were found to contain 100% horse mackerel, a third contained 96% (however the data file associated with this was corrupted) and the remainder were less than 89% horse mackerel. 60 schools were detected between and within the two 100% regions and S_v data were exported for these areas of the echogram only (Figure 2). On inspection the S_v histograms were found to be broad but approximately normally distributed (Figure 1).

One trawl contained a high abundance of pilchard (55% by mass) and no other fish. However, the net also contained many *A. aequorea* (45%). When the S_v histograms were inspected for this region two distinct modes were apparent, particularly with the 18-120 kHz frequency difference (Figure 1). The upper mode corresponded to that found from *A. aequorea* only data, therefore we supposed that the lower mode was due to pilchard. To separate the two modes, we filtered the S_v data for echoes due to *A. aequorea* using the newly calculated confidence interval and attributed the remaining backscatter to the pilchard (Table 2). When S_v -difference histograms were re-inspected using this filtered data the lower mode was observed to dominate. However, thick upper tails were evident in the 18-38, 18-120, and 18-200 histograms indicating that the *A. aequorea* filter may miss some echoes due to these jellyfish. The *A. aequorea* filter was not altered because we aim to minimise misallocation of fish backscatter to jellyfish, which might dominate the S_v .

So, four sets of normally distributed S_v -difference histograms were created using selected data, pooled by species. The scaled 95% confidence interval of the S_v data were then used to parameterise the filters, which can be used to classify non-trawled areas.

Target Strength

The distribution of single target detections for *C. hysoscella* is broad, reflecting the wide size-distribution sampled (Figure 6). In contrast, the relatively narrow size-distribution of *A. aequorea* corresponds to a more normally distributed TS distribution. The horse mackerel sample also shows a narrow size-distribution but the TS distribution is much broader indicating that the filter may not be rejecting non horse mackerel targets. The pilchard detections were found within a layer that was not as dense as the horse mackerel schools and here many more single targets were found. The histogram of pilchard targets at 38kHz is skewed and has a thick lower tail with dB values below that expected for pilchard (Barange et al. 1994).

Three of the *C. hysoscella* single target detections, and none of the *A. aequorea* or fish targets, were found to match by angular position across the four frequencies. This is probably due to the relatively low density of *C. hysoscella* swarms enabling more targets to be distinguished. When the limiting 200 kHz data was excluded, 3 horse mackerel targets matched. However, no matches were found for *A. aequorea* or pilchard. The 18 kHz data was subsequently excluded and matches for *A. aequorea* and pilchard were made over the two remaining frequencies (38 and 120 kHz). The 18 kHz data was chosen for exclusion since the 18 kHz beam was the widest and most likely to detect multiple targets, which would inhibit matching.

Discussion

The histograms of dB-difference for the two fish species were always broader than those of the jellyfish; the horse mackerel histogram may be wide due to orientation effects whereas the pilchard histogram may be incorporating some backscatter from *A. aequorea* (Figure 1). Each of the *C. hysoscella* histograms show slight deviations from normality in their tails, which are elevated where the distribution overlaps those of horse mackerel and *A. aequorea*, indicating very low level contamination as expected from the trawl catch which were never solely *C. hysoscella* (Figure 1). The pilchard filter appears to separate from all of the others at 18-38 kHz and with increased sample size this filter may be

substantially improved. The horse mackerel and *A. aequorea* filters are generally co-located on the x-axis, however, both separate remarkably well from *C. hysoscella*. In practise, the *A. aequorea* filter will merely produce a subset of the horse mackerel filter, since the entire range of the *A. aequorea* filter is within that of the horse mackerel. This actually proves to be a greater problem for filtering horse mackerel than *A. aequorea*, since the horse mackerel filter will always make detections even if there are only *A. aequorea* present whereas the *A. aequorea* filter may only part-sample horse mackerel incorrectly. This can be demonstrated through use of the filters over the echogram in the region of the horse mackerel schools. In Figure 3, we see that the horse mackerel filter successfully identifies backscatter from the schools, while the *C. hysoscella* filter detects nothing, and the *A. aequorea* filter produces very few detections, and the pilchard filter appears to misidentify the horse mackerel. In the area of a dense *A. aequorea* aggregation, as identified by trawling, the jellyfish filters are again successful (Figure 4a). However, the horse mackerel and pilchard filters are inadequate, as currently defined, since many detections are found within the trawl area that found 100% by mass of *A. aequorea* (Figure 4b). Once, the data are reduced so that only S_v values >70 dB are passed to the fish filters, the outputs appear convincing. Figure 5a displays a trawled area that netted 89% *C. hysoscella*, 10% horse mackerel, and 1% *A. aequorea* by mass. From the unfiltered echogram, it is apparent that the trawl may have sampled a couple of horse mackerel schools in addition to the medusae in the aggregation. The *C. hysoscella* filter successfully identifies many data points (Figure 5b) and the *A. aequorea* filters a small amount as expected (Figure 5a). The horse mackerel filter appears to correctly identify backscatter from the schools but there are many detections throughout the water column also, which may or may not be fish (Figure 5b). When a minimum threshold of -70 dB is applied to the data the schools become readily distinguishable and using this data only the horse mackerel filter appear convincing as before. Again the pilchard filter appears to misidentify the horse mackerel (Figure 5b).

Figure 5 displays a trawled area that netted 68% pilchard and 31% *A. aequorea* by mass. Here the pilchard, *A. aequorea*, and *C. hysoscella* filters appear to make successful detections (Figure 5a and b). However, the horse mackerel filter appears to be in error. Once the minimum data threshold is again set to -70 dB these detections are lost indicating that there do not actually appear to be any horse mackerel schools in the trawled area.

Single Targets

Both jellyfish TS distributions agree with our previous single target estimates (see Brierley et al. 2004; 2001). Individual medusae show great variability in their TS, probably due to pulsation of the bell. At 38 kHz, Brierley et al. (2004) recorded backscatter from tethered medusae and found that the mean TS for a 47 cm *C. hysoscella* was -55 dB, but that the same medusae could produce TS values up to -43 dB and down to -69 dB, while a 19 cm medusae had a mean TS = -62 dB, a max of -56 dB, and a min -73 dB. A 24 cm *A. aequorea* medusae was recorded with a mean TS = -50 dB, max -47 dB, and min -60 dB, while a 19 cm had a mean TS = -65 dB, max -62 dB, and min -70 dB.

Very few S_v -filtered single targets also matched by angular position, but those *C. hysoscella* matches suggest that the peak in the distribution shown at high TS at 18 and 38 kHz are due to single targets and are not a result of combining multiple echoes. The same cannot be said for the 120 kHz and 200 kHz distributions. At these higher frequencies there is no defined peak and the distribution at 200 kHz becomes skewed to lower TS values. The *A. aequorea* targets that matched by angular position between the 38 and 120 kHz frequencies were located at or near the centre of the distribution, therefore the most likely TS at 38 kHz is indeed the modal value.

The TS distribution at 38 kHz for horse mackerel is below that expected (TS -26 to -55 dB, with mean TS reported as -37 to -40 dB for 28 cm individuals, Barange et al. 1994). We netted smaller fish, total length 9 to 14 cm, but these fish should still have a TS of -48 to -44 dB respectively, according to the TS-length relationship

published by Barange et al. (1994). It is possible that the low single target detections of -55 dB are from small (4 cm) horse mackerel that were present but not sampled by the large mesh of the net. However given that the distribution is centred on much lower values, this is considered unlikely. The overlap of the horse mackerel distribution with those of *A. aequorea* and pilchard suggests that other targets are being included by this filter. Only 1 match was made over the three frequencies where detection were found and this target has a TS at 120 kHz matching with central values in the 38 kHz distribution and high values in the 18kHz distribution, which indicates that the high TS values at 120 kHz could be fish targets that were not detected at the lower frequencies. These high TS values at 120 kHz overlap the *C. hysoscella* TS distribution and could indicate that the *C. hysoscella* filter has included some horse mackerel targets, perhaps explaining the skewed peaks at 18 and 38 kHz in the *C. hysoscella* TS distributions. However, when the *C. hysoscella* filter was applied to the horse mackerel echogram area no detections were made, therefore these filtered TS are most likely *C. hysoscella* targets (Figure 2b). Horse mackerel targets were exported from school areas to minimise the misallocation of S_v but this may, in fact, have reduced the detectable number of individual targets since the school is so dense that most targets are not resolvable individually. Since the radius of the beam here ranged from 2.5 to 4.2 m, for 38 and 18 kHz frequencies respectively, by using these data we have limited the single target detection to locations near to the edge of the school or nearby, which are less likely to be the targeted fish than those within the school.

Barange et al. (1994) report pilchard TS values ranging from -50 to -30 dB, which agrees with the higher TS values found here in regions of echogram identified by the pilchard filter. The lower values may be due to *A. aequorea* and the TS between -55 and -57 dB might also be due to *Sufflogobius* (Barange et al. 1994). Only 2 targets in the pilchard TS distribution matched by angular position between the 38 and 120 kHz frequencies. These matches are in the lower tail of the 38 kHz distribution of pilchard TS and may in fact be due to *A. aequorea*. The

peak in this distribution near -50 dB, and those values above, could represent the pilchard.

So, both jellyfish filters appear to identify single targets correctly, but the fish TS distributions appear to include non-target species. This was expected as the fish S_v -difference filters failed to exclude areas of the echogram where trawling indicated that fish were not present. However, increased sampled size would justify the use of a narrower filtering interval and thus greater discriminatory power. Dense fish schools may be distinguished from jellyfish swarms on the basis on their echo strength alone. Nevertheless, improved filters are required to successfully distinguish non-schooling fish.

We have produced four S_v -difference filters based on the response of jellyfish (*Aequorea aequorea* and *Chrysaora hysoscella*) and fish (*Sardinops ocellata* and *Trachurus trachurus capensis*) to four frequency insonification. When this information is used to filter the echo data, the two species of jellyfish separate from each other remarkably well (Figures 3a and 4a). *C. hysoscella* is also easily distinguishable from horse mackerel and pilchard (Figure 2b, 4b and 5b). While, *A. aequorea* appears to be distinguishable from fish (Figure 2b, 4a, and 5a), fish are not so easily distinguished from aggregations of *A. aequorea* (Figure 2b and 3b). However, horse mackerel schools are strong scatterers, generally producing backscatter at higher levels than jellyfish swarms, and may be separated from jellyfish by their echo strength alone or through the detection of individual schools (Figure 2). Dispersed aggregations of fish, such as those found for pilchard (Figure 5), may prove harder to distinguish from jellyfish and may therefore serve as a source of error in biomass estimation of jellyfish and horse mackerel.

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Figures and Tables

- Figure 1 S_v -difference histograms for *C. hysoscella* (red lines), *A. aequorea* (blue lines), horse mackerel *Trachurus trachurus* (black lines), and pilchard *Sardinops Ocellatus* (green lines), showing the 18-120 dB histogram for pilchard and *A. aequorea* combined (light blue line).
- Figure 2a Echograms showing trawled area (yellow hashed area) that netted 100% horse mackerel fish. S_v data with min threshold at -110 dB (top), -70 dB (middle), and filtered for horse mackerel (bottom).
- Figure 2b Echogram with min threshold at -110 dB filtered for *Chrysaora hysoscella* (top), *Aequorea aequorea* (middle), and pilchard (bottom).
- Figure 3a Echogram showing trawled area (yellow hashed area) that netted 100% *Aequorea aequorea* medusae. S_v data with min threshold at -110 dB (top), filtered for *Aequorea aequorea* (middle) and *Chrysaora hysoscella* (bottom).
- Figure 3b S_v data filtered for pilchard (top), horse mackerel (middle), and for horse mackerel with min threshold set to -70 dB (bottom).
- Figure 4a Echogram showing four ringed fish schools (yellow/orange loops) and trawled area (yellow hashed area) that netted a high density of *Chrysaora hysoscella* medusae with some horse mackerel fish. S_v data (top) filtered for *Chrysaora hysoscella* (middle) and *Aequorea aequorea* (bottom).
- Figure 4b S_v data filtered for pilchard (top) horse mackerel (middle) and with min threshold set to -70 dB filtered for horse mackerel (bottom).
- Figure 5a Echogram showing trawled area (yellow hashed area) that netted a high density of pilchard (68% by mass) and *Aequorea aequorea* (31%) medusae with a few *Sufflogobius* fish (1%). S_v data with min threshold at -110 dB (top) filtered for pilchard (*Sardinops ocellatus*) (middle) and *Aequorea aequorea* (bottom).
- Figure 5b S_v data with min threshold at -110 dB filtered for *C. hysoscella* (top) and filtered for horse mackerel at -110 dB (middle) and -75 dB (bottom).
- Figure 6 Probability distributions of filtered TS for *A. aequorea*, *C. hysoscella*, horse mackerel, and pilchard and associated size distributions (umbrella diameter for jellyfish and total length for fish). The individual black, grey, and cyan bars indicate those values where 1 detection also matched by angle across a number of frequencies; for *C. hysoscella* 3 targets matched over all 4 frequencies, for horse mackerel 1 target over 3 frequencies (not 200 kHz) and for *A. aequorea* 1 target and pilchard 2 targets over 2 frequencies (38 and 120 kHz) only.

Table 1	Beam volume standardisation and corresponding dB reduction
Table 2	Smoothing weights for 5x5 gaussian convolution
Table 3	The S_v -difference intervals used for filtering for each species.
Table 4	The number of detections once filtered and the number of measured medusae.

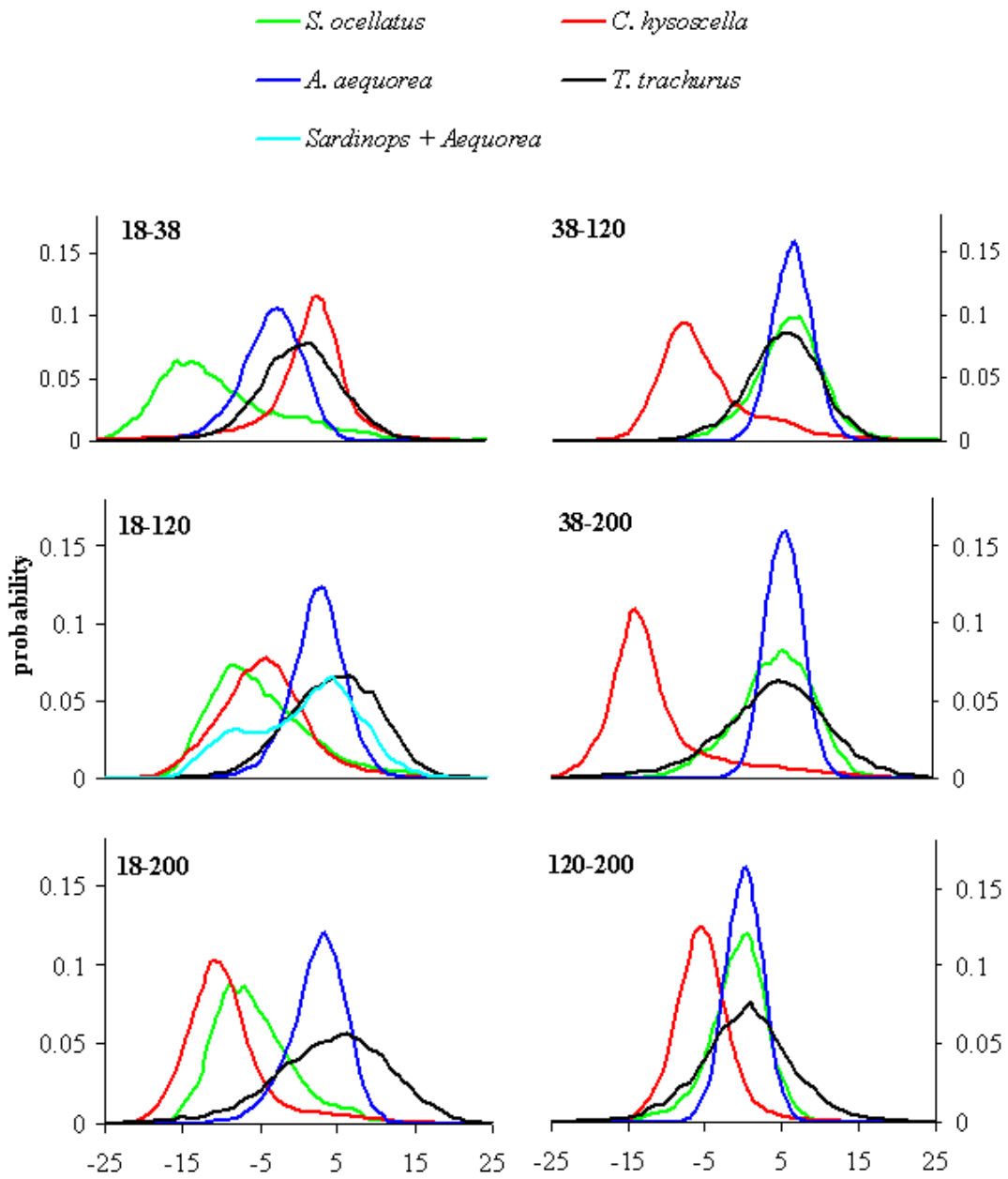


Fig 1 Multifrequency S_v histograms of dB difference



Fig 2a: Horse mackerel area data (top) with min threshold at -70dB (middle) filtered for horse mackerel (below)

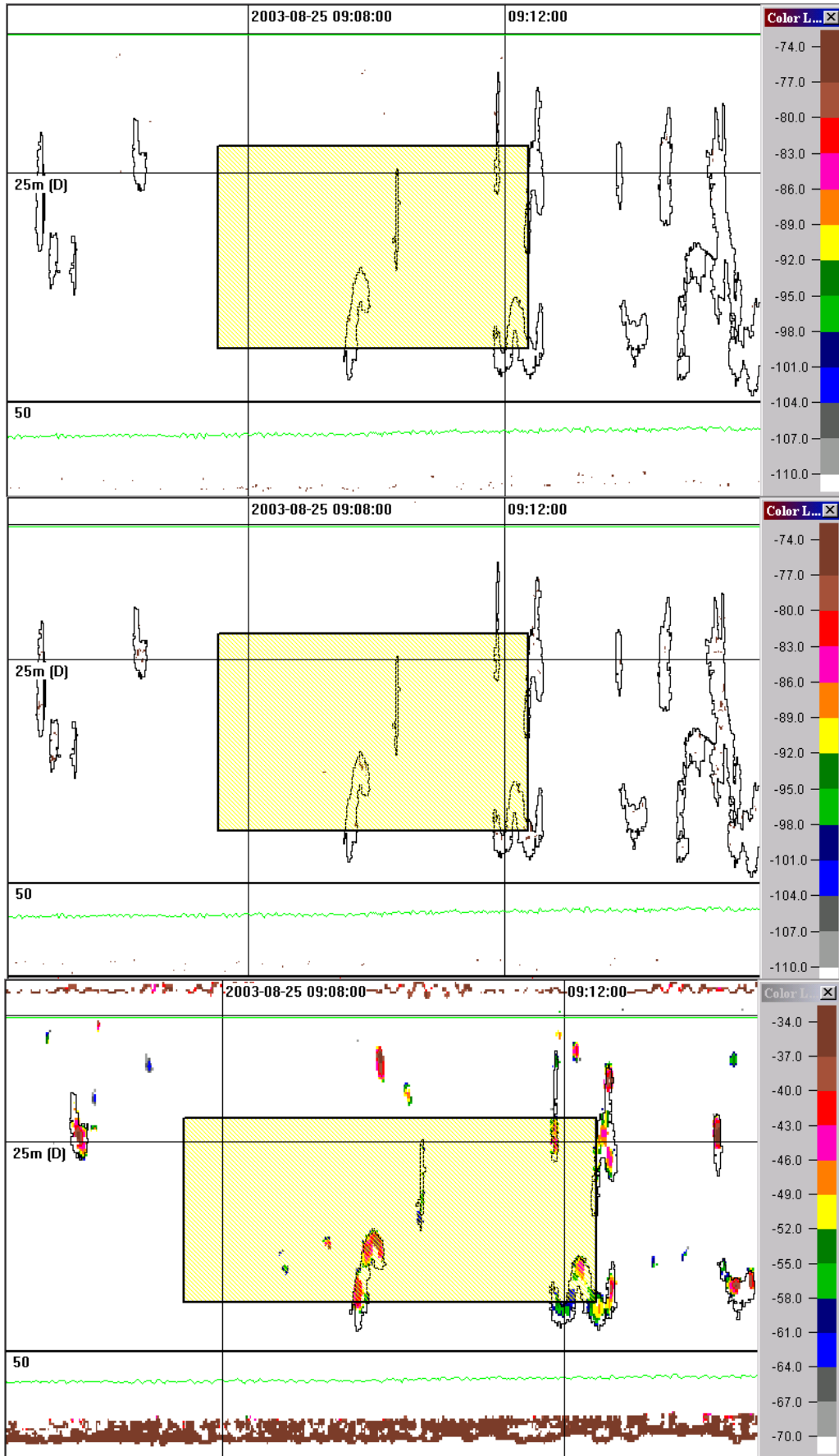


Fig 2b Horse mackerel area filtered for *C. hysoscella* (top), *A. aequorea* (middle) and pilchard (bottom)

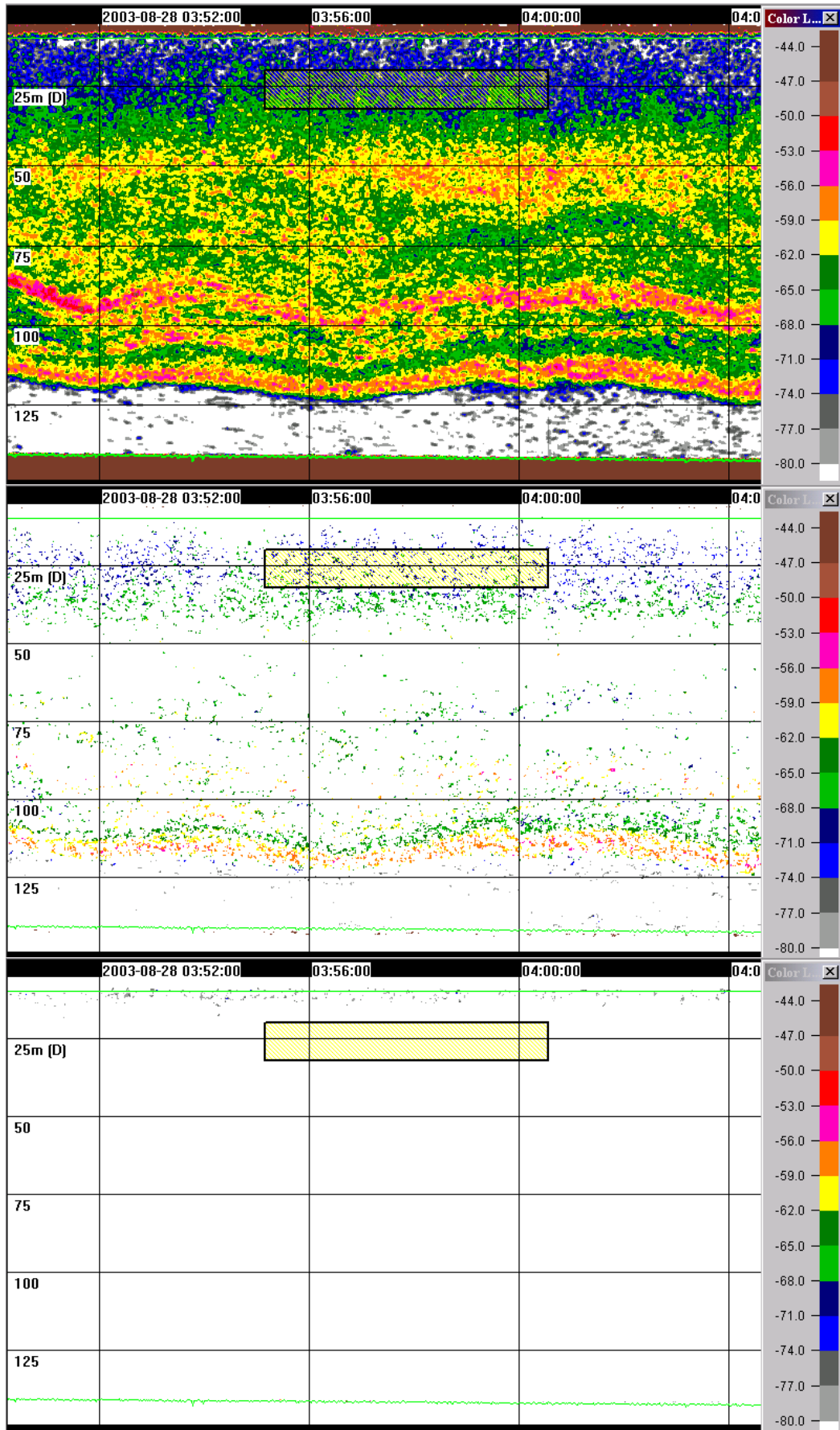


Fig 3a *A. aequorea* area data (top) filtered for *Aequorea aequorea* (middle) and *Chrysaora hysoscella* (bottom).

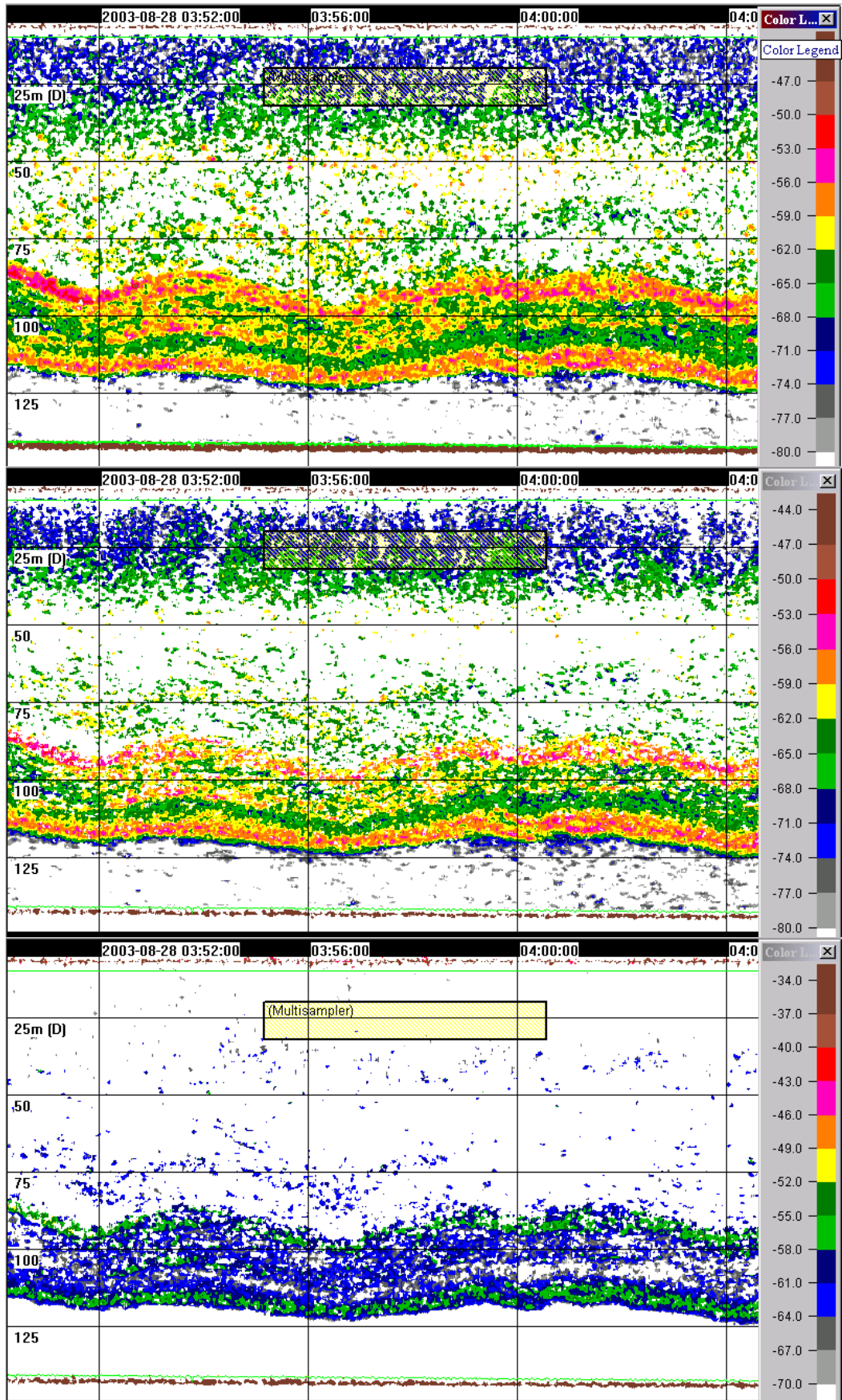


Fig 3b: *A. aequorea* area filtered for pilchard in (top), horse mackerel (middle and bottom with -70dB threshold)

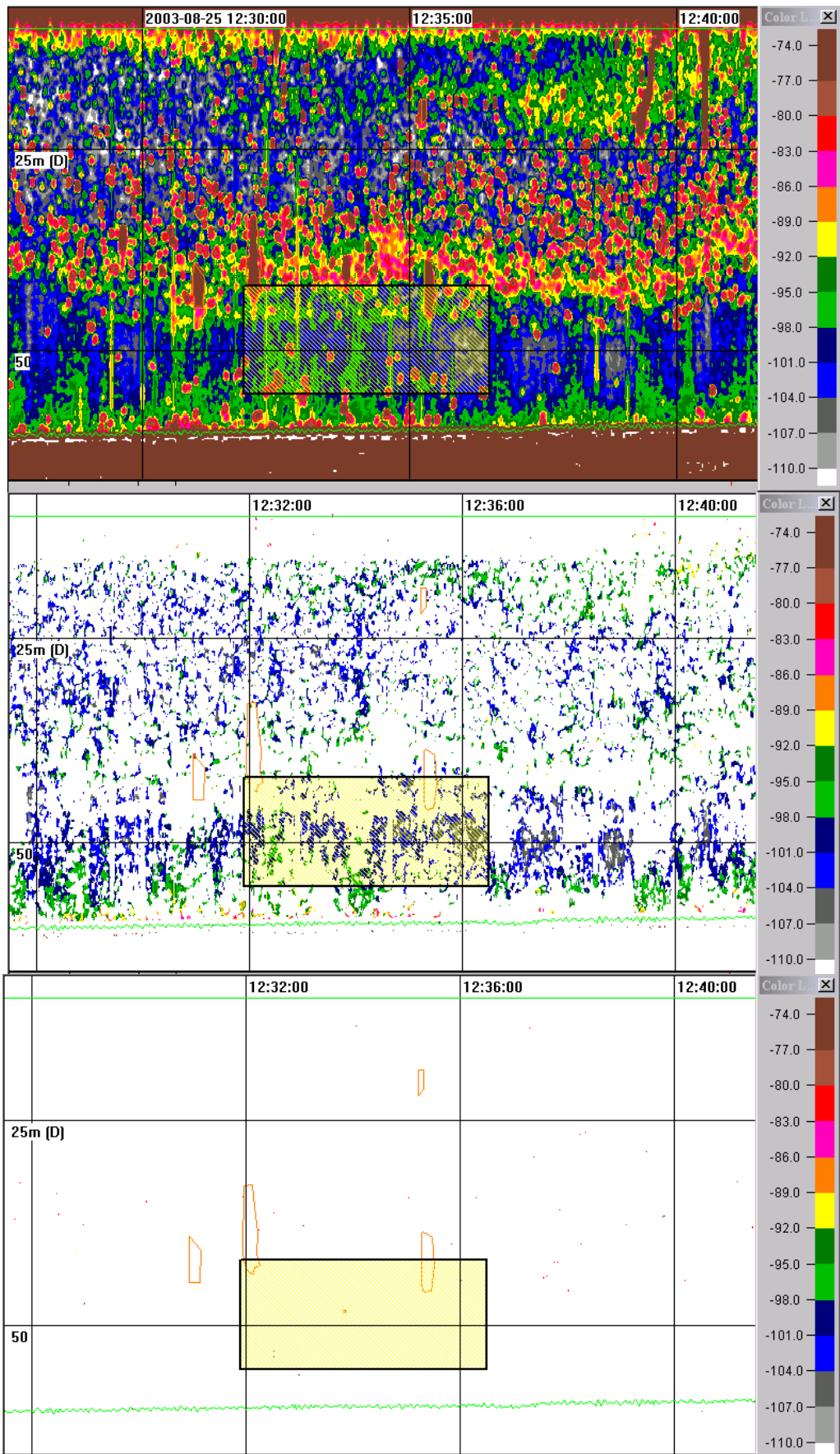


Fig 4a: *C. hysoscella*/horse mackerel area data (top) filtered for *C. hysoscella* (middle) and *A. aequorea* (bottom).

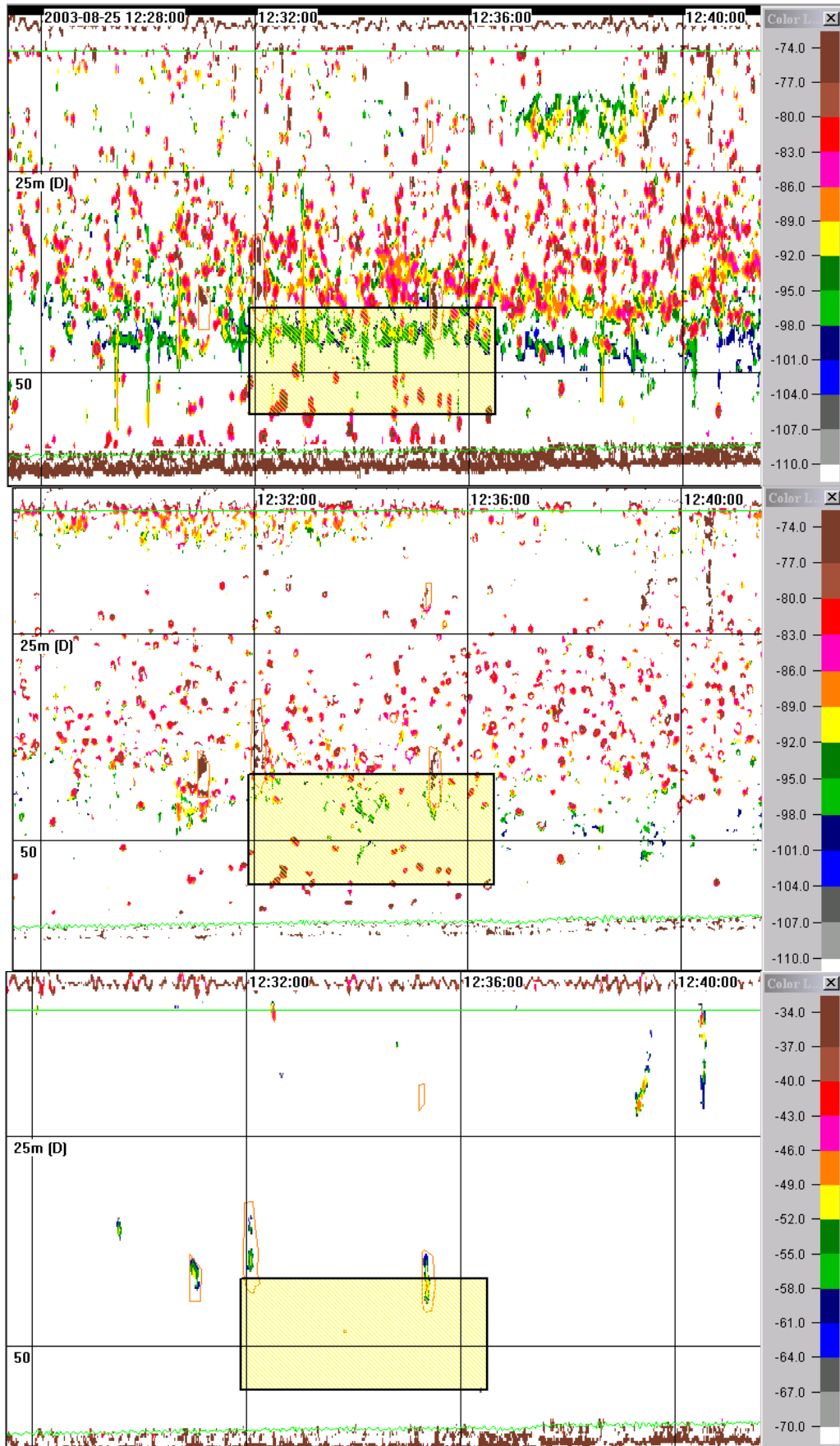


Fig 4b: Filtered data for pilchard (top) and horse mackerel (middle and bottom with -70dB threshold)

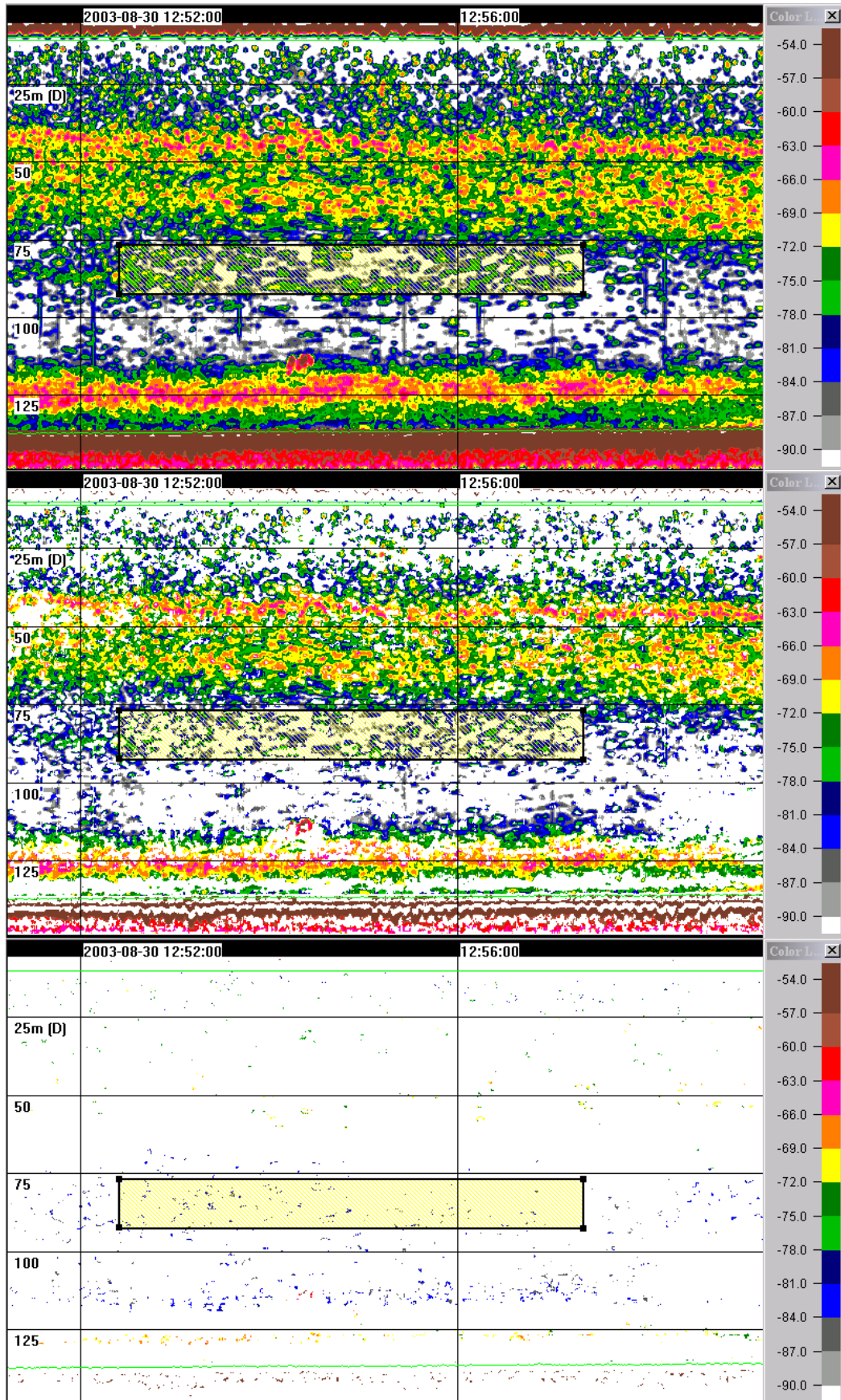


Fig 5a Pilchard/*A. aequorea* area, data (top), pilchard detections (middle), and *Aequorea aequorea* detections (bottom)

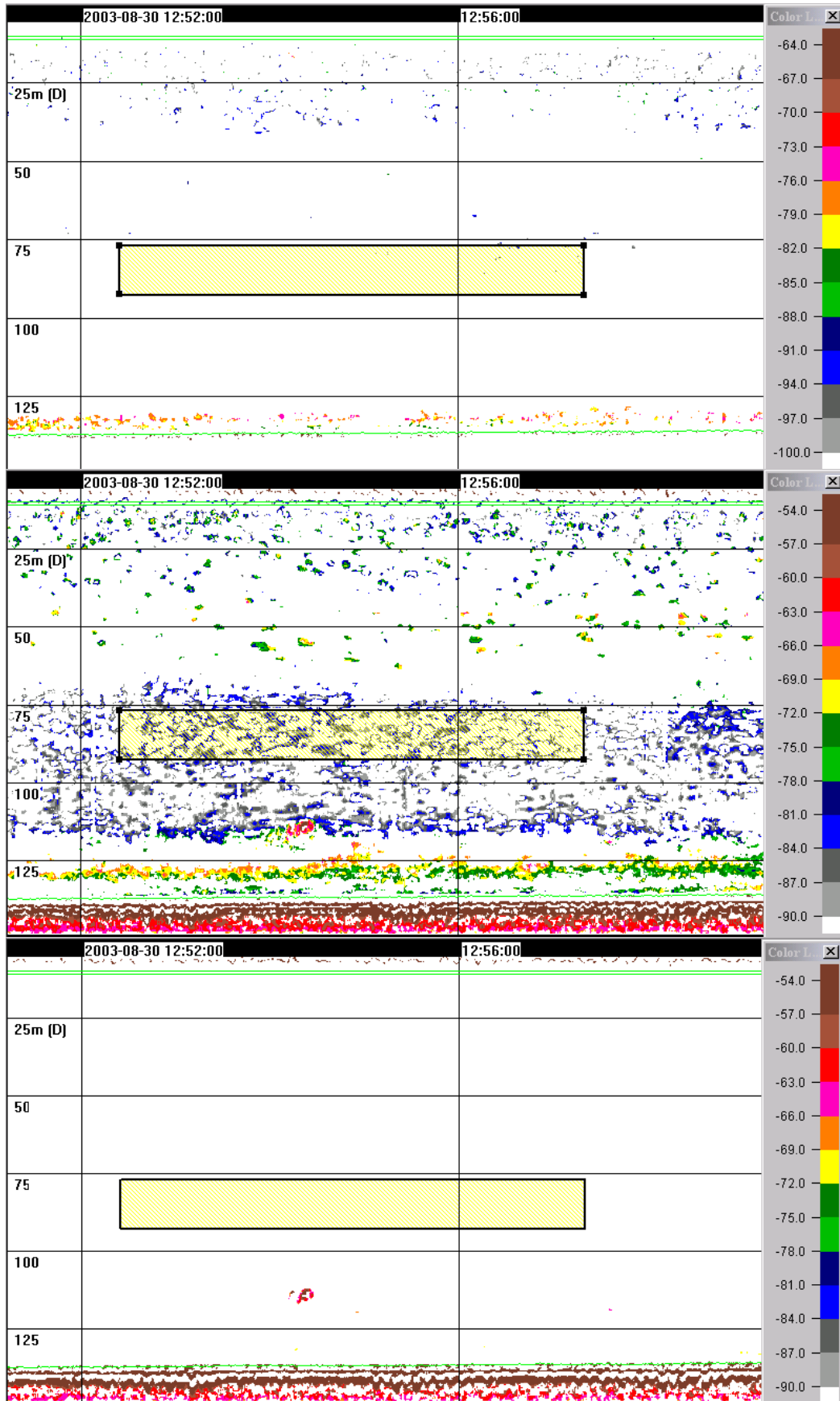


Fig 5b *C. hyoscella* (top) and horse mackerel detections (middle and bottom with threshold -70dB)

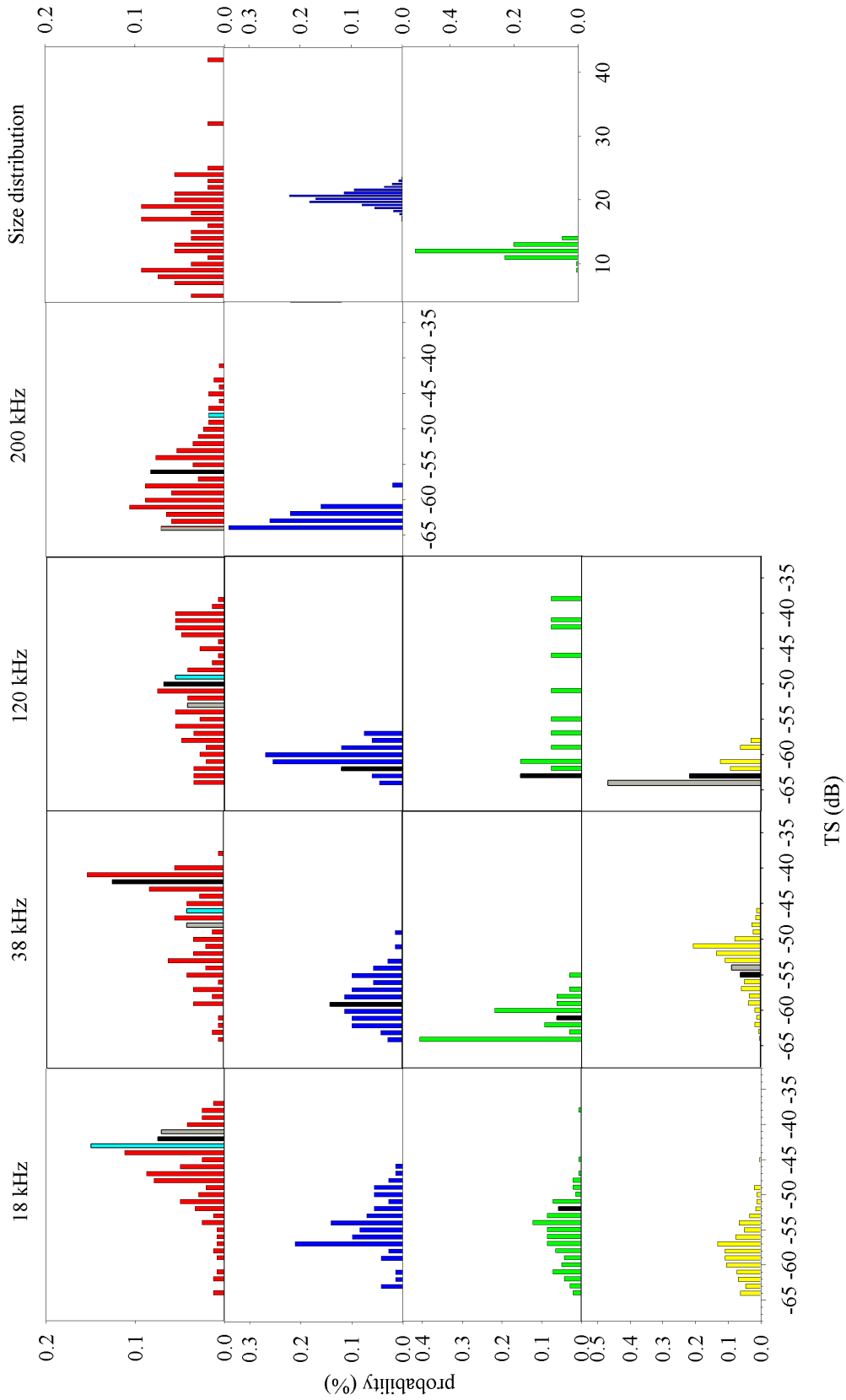


Fig 6 Filtered TS and size distributions for *A. aequorea*, *C. hysocella*, horse mackerel, and pilchard.

Frequency	18 kHz	38 kHz	120 kHz	200 kHz
Actual/reduced volume ratio	2.601	1	1.112	1.044
dB reduction	4.151	0	0.463	0.188

Table 1

0.0091	0.1738	0.6569	0.1738	0.0091
0.1738	0.3385	0.8216	0.3385	0.1738
0.6569	0.8216	1.3047	0.8216	0.6569
0.1738	0.3385	0.8216	0.3385	0.1738
0.0091	0.1738	0.6569	0.1738	0.0091

Table 2

S_v difference (dB)	18-38	18-120	18-200	38-120	38-200	120-200
<i>Chrysaora hysoscella</i>	6.85	0.25	-6.65	-2.59	-9.09	-2.39
	-2.00	-10.92	-16.22	-12.94	-18.63	-9.80
<i>Aequorea aequorea</i>	0.09	5.11	4.91	7.45	7.03	1.63
	-6.29	-0.58	-1.02	3.28	3.05	-2.27
Horse mackerel	8.00	12.56	14.13	10.87	13.68	8.49
	-6.72	-3.85	-6.69	-2.57	-6.23	-8.70
Pilchard	6.55	8.40	5.16	14.41	14.49	6.91
	-24.94	-17.58	-16.46	-3.59	-5.94	-8.22

Table 3

Species	Frequency (kHz)				Size distribution (bell diameter, cm)
	18	38	120	200	
<i>Chrysaora hysoscella</i>	241	142	146	170	54
<i>Aequorea aequorea</i>	71	71	67	50	911
Horse mackerel	139	32	13	0	179
Pilchard	257	338	32	0	-

Table 4