

## SEARCHING FOR DEEP SEA SQUIDS

M. R. Clarke

'Ancarva', Southdown, Millbrook, Torpoint, Cornwall, PL10 1EZ, UK, malcolmclarke@sapo.pt

### ABSTRACT

The author outlines his experience in searching for, finding and catching oceanic squids over a period of 44 years. This has involved using a wide variety of fishing gears and techniques.

### INTRODUCTION

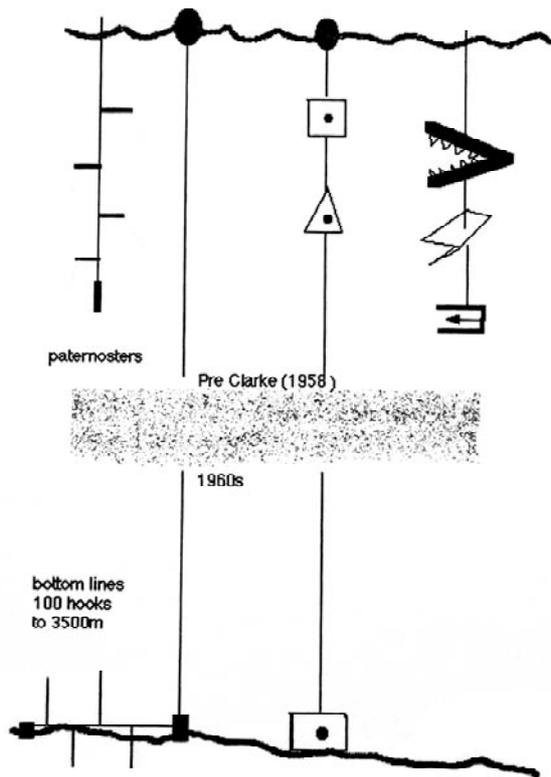
In 1958, when the author started a career at the National Institute of Oceanography, Surrey, England, oceanic squids were rarely caught, poorly known and sparsely studied. His brief, in this new job, was 'Find out more about oceanic squids'. His tools were a ruler, a dissection kit and the regular use of an old ship, with a proud Antarctic history, RRS 'Discovery II'. His fellow scientists had much experience at sea and were enthusiastic helpers in his aims, although they had had limited success with catching squids. This was the start of 30 years with 3 months at sea almost every year and a further 15 years with less regular seaborne endeavours. Such a long period gave him a leisurely opportunity to try many methods to observe, catch and try to catch oceanic squids. Each method brought different species, different data, different problems and different salutary lessons.

The tradition within the Institute was that biologists developed their own gear, paid close attention to its manufacture and handled all their own gear over the side and personally used all winches except the largest, during trawling and other sampling operations. This gave them a clear perception of what can be done with particular gear, why it functions as it does and how catches can be improved. All ships' movements and operations on deck were directed by the scientists who were helped immensely by the netman and bosun and, if one was present, by the trawling skipper.

### METHODS AND RESULTS

#### *Observations, hooks and traps*

Early cruises in the North Atlantic between the Azores and the Cape Verde Islands showed that a few genera of squids were fairly regularly found floating, dead, at the sea surface. In particular, adults of *Histioteuthis* and *Alloposus* (*Haliphron*) were found and subsequent experience has verified this observation. Indeed, at that time, six or so species of *Histioteuthis* were only known from collection of dead animals. The occurrence of these floating dead near Madeira and the Azores, where sperm whales feed, has led to the author's assumption that the two observations are linked. On an early cruise a 1m long cranchiid squid was found dead. This was three times the size of the currently described species of the family with the exception of a specimen in the Paris Museum named *Phasmatopsis cymoctypus*. From notes made of that specimen by Dr Anna Bidder the author referred his specimen to the same species. However, there has always been doubt concerning its identity and its relationship with another genus, *Megalocranchia*, which has subsequently been found to have very large members. Unhappily, the type (Paris) specimen has now been lost. *Architeuthis* is sometimes found floating dead, but not by the author, and comes ashore from Iceland to Senegal.

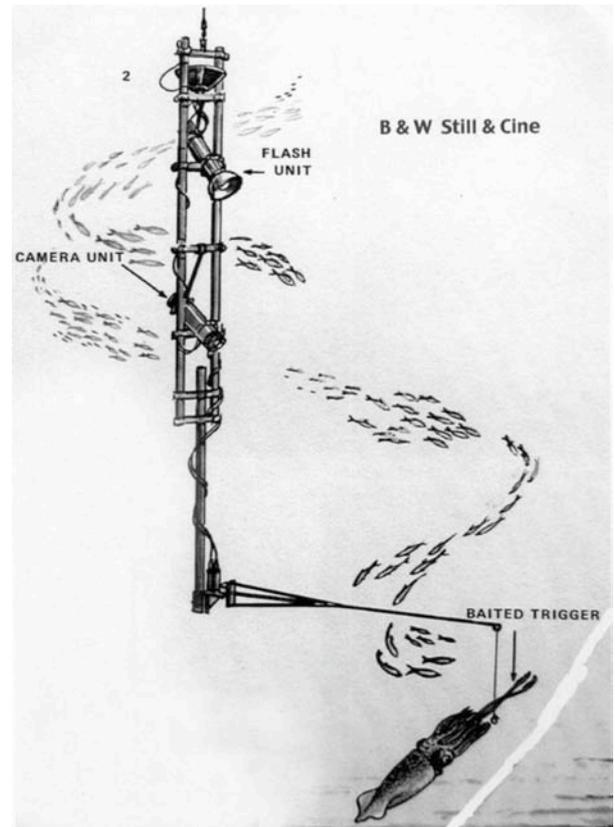


**Fig. 1** A variety of traps and line configurations used to catch midwater squids by National Institute staff in 1950s and 60s

Regularly squids come to lights at night and, sometimes, even fly from the sea in daylight. These are almost invariably ommastrephids; in the North Atlantic *Ommastrephes bartrami*, *Sthenoteuthis pteropus* and *Todarodes sagittatus* (North of 45°N) and in the Indian Ocean, *S. oualaniensis*. The exception was the occasional appearance of *Onychoteuthis*. These species were caught with handnets and handlines equipped with jigs of various designs either incorporating bait as in Madeira or, without bait, as used by the Japanese.

Prior to the author's employment, NIO staff collected ommastrephids at the surface but also used a variety of midwater traps and droplines with various baits including bacon, squids, herrings' tails and lights. Traps included artificial whale jaws (with white or luminous teeth), wire netting and spears. None of these were successful (Fig. 1).

From the 1950's, colleagues, and then the author, lowered baited still and cine cameras into midwater in the upper 1000 m (Fig. 2). We found *Todarodes*, deeper than 300 m, and *Ommastrephes* and *Sthenoteuthis* were the only subjects photographed except for one or two fish.



**Fig. 2** The baited still camera used to photograph deep sea squids

The author obtained a long line hauler and dropped a line on bottoms up to 3500 m deep bearing up to 100 hooks on snoods attached to a horizontal line on the bottom. The lines to the surface were buoyed off for six or so hours. Many dozens of hauls produced many hundreds of spectacular fish but only one cephalopod and that was a *Cirrotheuthis*, foul hooked through its fin.

A dozen or so times, large baited, rectangular, wire traps were placed on the bottom at depths of 500 - 1500 m. These only caught fish which, at 500 m, were always gnawed down to the bone by amphipods.

Since other observations indicate that there are cephalopods at the depths fished, most of the above observations lead to the conclusion that cephalopods, with the exception of ommastrephids, do not eat dead food.

### Nets

Prior to the author's involvement, a standard 70 cm diameter ring net, was opened and closed (by a brass 'messenger') while being hauled vertically to investigate vertical distribution of very small animals

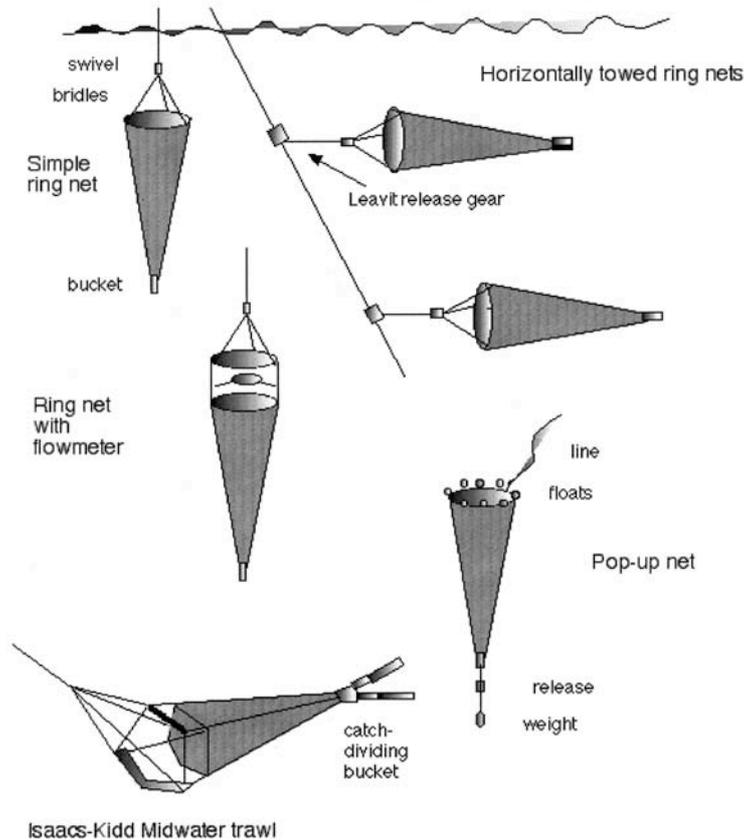


Fig. 3 Ring nets used in 1959 - 64, a pop-up net and an Isaacs-Kidd midwater trawl

and larvae. Before the Indian Ocean expedition (starting 1963), colleagues developed a standard 1 m ring net for hauling to the surface from a depth of 200 m at a haul rate of 1m/sec. When properly used, the 70 cm nets gave good comparisons between depths and areas. The Indian Ocean standard net was used by a large variety of ships but a cursory observation of the samples showed that some ships were incapable of standing still during hauling so that hauls should not be regarded as comparative, particularly between ships and bridge officers. Catches vary greatly according to the orientation of the net; whether it is pulled vertically, horizontally or obliquely. Ring nets have bridles (Fig. 3), sometimes opening-closing gear and flow meters in front of the mouth which push the water ahead of the net so that the only animals caught are small and slow swimming and the numbers are very small; they catch pathetically few tiny paralarvae of squids.

To overcome the bridle problem and the limitation on net diameter imposed by hauling vertically with a winch, the author developed pop-up ring nets (Fig. 3). These were ring nets, having circular mouths, which were carried down, bucket-first, to a depth of 1000 m

by a weight which was released by a shear pin device operated by pressure. The buoyant floats around the mouth then brought the net back to the surface. These showed promise and had the distinct advantage that they could be used from a small boat with no winches. Their disadvantage was that rate of fishing was dependant on the amount of buoyancy and this had to be more than matched by the weight. Thus, the faster the fishing, the greater the weight which must be handled over the ship's side. Also, some closing device had to be incorporated to prevent the buoyant part of the catch from rising to the sea surface and drifting out of the mouth when the net reached the surface. Nets rising at 1 knot provided animals which were alive or in excellent condition. The nets were most easily found, after surfacing, by attaching a nylon thread and a light to the mouth. Few squids were caught in the dozen or so hauls made.

Where were the paralarvae of the ommastrephids we saw at the surface, as well as all the other squids?

For horizontal trawling, the bridle problem was reduced by trying bongo nets which had a ring net either side of a central warp; we still caught very few small squids, largely enoploteuthids, pyroteuthids and

cranchiids with small adults (*Abraliopsis*, *Pyroteuthis*, *Pterygioteuthis*, *Cranchia*, *Liocranchia*, *Helicocranchia*) and a few paralarvae.

A colleague, Peter David, developed a special neuston net which fished, on a calm day, the top 15 cm of the sea. This caught very few tiny paralarvae of squids in hundreds of hauls even though it divulged the special blue life of the surface and distinguished between what was living in the top 5 cm from lower down. The author tried a few trials with an air lift fixed to the rear of a net dragged along the sea surface at night. This caught three small fish which had only been caught deeper than 1000 m before, but no squids.

During darkness it was usual to drag a 1 m ring net through the surface at any time the ship was steaming less than 4 knots (i.e. while trawling other nets). This afforded a constant supply of small animals and larvae for experiments. While individual larval squid were fairly regularly caught, only very occasionally were they in numbers to suggest a shoal had been sampled.

On a cruise in 1959, an attempt was made to study vertical distribution and diel migration of midwater animals by using 2 m ring nets; three nets were towed 400 m apart from one warp and were opened and closed by messengers sent down the warp. It proved very difficult to obtain even one 'round the clock' collection due to mechanical failures of the opening-closing device and by the fact that the 'jelly' *Pyrosoma* collected on the warp and cushioned the messenger so that it did not operate the release gear. Few squid were caught, probably because of the net bridles and closing gear in front of the mouths.

Prior to, and just after the author's involvement, colleagues used an Isaacs-Kidd Midwater trawl with a 3 m wide depressor (Fig. 3). With research into vertical distribution in mind, Peter Foxton had added a forked tube with a flap so that animals could be caught in a bucket attached to one side as the net was paid out and brought in and into another bucket as it was fished horizontally at 2 - 3 Knots. The flap was first operated by a mechanical pressure device and later by electronics and an acoustic signal from the ship. As this net had a mouth of 7 sq.m it caught larvae and adults of enoploteuthids, pyroteuthids and some cranchiids and young of a few other midwater species such as histioteuthids and onychoteuthids, but all less than about 10 cm long and in numbers only averaging about 4 per haul of two hours. The oblique parts of the tow

caught more squid than the horizontal and it became obvious that animals were held up in front of the flap and moved into the bucket only when the flap operated. Thus, horizontal tows were not discrete and the net was not good for studying vertical distribution.

Simultaneous with these developments the author chose to explore the use of larger, commercial, midwater trawls in the hope that their size (mouth > 250 sq.m) and speed (4 - 6 knots) would increase the number of squids sampled.

The British Columbia Midwater trawl (BCMT) with a square mouth 15 m across and 250 sq m. caught more of the species up to about 20 cm long and more of the rarer families than caught by the Isaacs-Kidd trawl.

To hold the mouth open, this trawl had two otter boards on long bridles which required careful balancing and proved difficult to handle on the RRS "Discovery II".

In 1963 RRS "Discovery II" was replaced by the larger RRS "Discovery" and the opportunity was taken to try a much larger trawl produced by Engels and with a mouth of 40 m x 20 m, 100 aluminium floats on its headrope, 500 kg of chain on its footrope and 2 Subergrub doors weighing 750 kg to hold the mouth open (Fig. 4). After a dozen or so nights of fishing this it became obvious that its use off a research vessel by scientists and crew who had no professional fishing experience was dangerous, very tiring and not over effective. Certainly more and larger squids were caught but three newly acquired ships with much better trawling facilities, the RRS "Challenger", RRS "Frederick Russell" and RS "Sarsia" became available for use by the author and, for some cruises, a fishing skipper. This permitted the use of other designs of otter trawl. Although they caught more of the smaller species and a few adults of histioteuthids, ommastrephids etc., cranchiids were usually represented by their reproachful eyes hanging on the netting and most squids were in poor condition due to the abrasion by the netting and the fish in the catch.

Interest of my colleagues was still mainly in sampling to show vertical migration. What was needed was a design of net which could fish in the same way in a large size range and at different speeds and be opening-closing. With the help of Arthur Baker, the

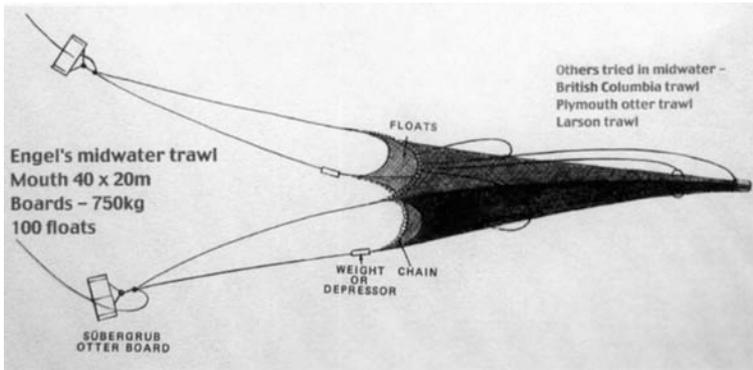


Fig. 4 The large Engel's otter trawl

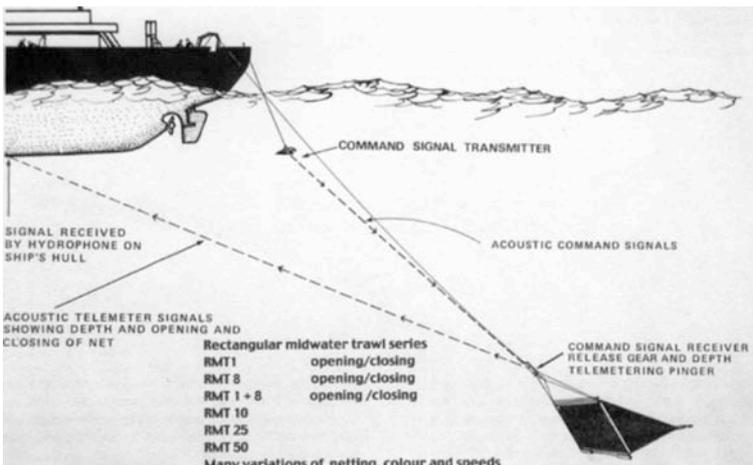


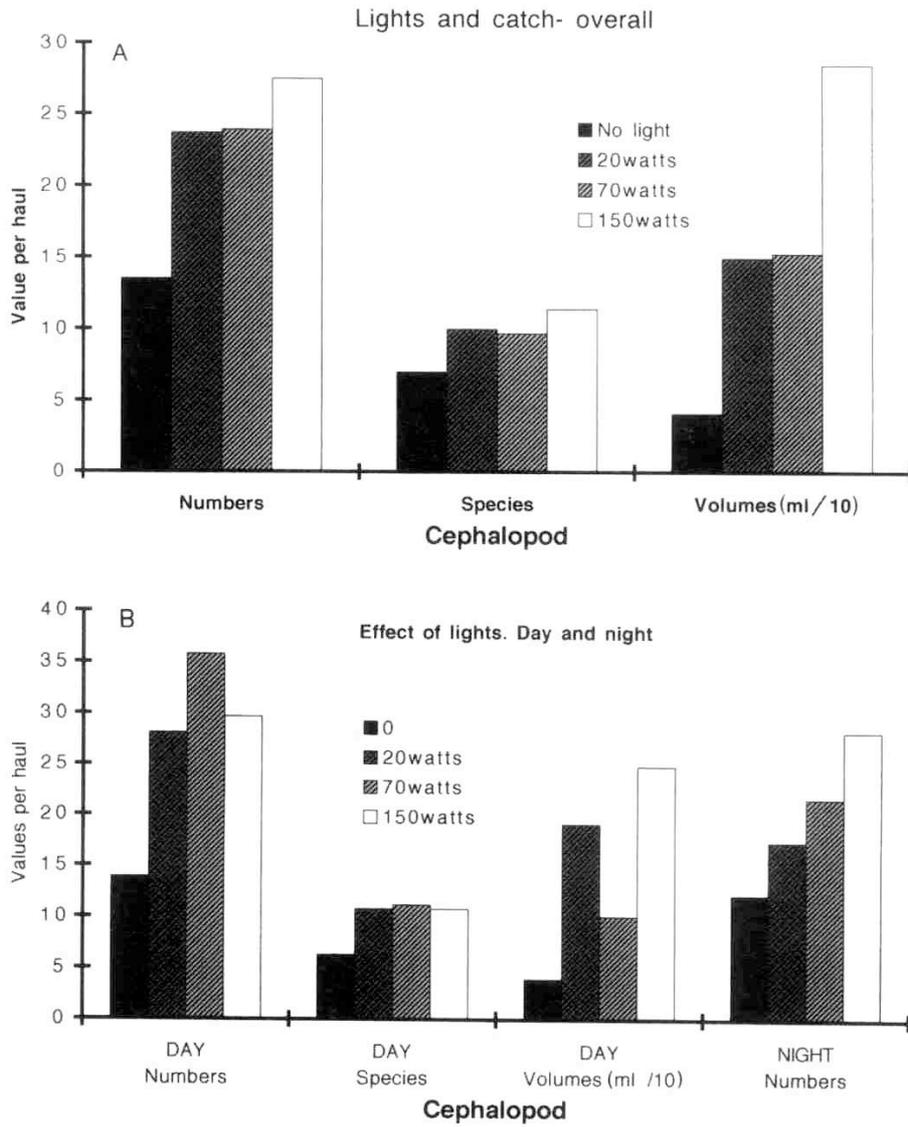
Fig. 5 The rectangular midwater trawls designed to sample a large size range of animals while fishing in the same way as well as opening and closing to study vertical distribution

author produced the Rectangular Midwater Trawl (RMT) with fishing mouths of 1/4 m, 1 m, 7 m, 8 m, 10 m, 25 m, 50 m and 90 m and we fished them with a variety of knitted netting from 0.3 - 2 cm and at speeds of 1/2 - 5 knots (Fig. 5. Clarke 1969, Baker *et al.* 1973). They caught a good range of squids, increasing body size with net size and the RMT50 proved a good compromise between handling and catching squids up to 30 cm. The catch was in better condition than comparable nets although increased speed produced more variety of squids but more damage. By acoustic control and monitoring the combination nets RMT1 + 8 m were controlled to fish very accurately between depths as little as 10 m apart, and day and night series of hauls at 50 - 100 m horizons were completed to over 1200 m at six latitudes in the north west Atlantic (Lu & Clarke 1975).

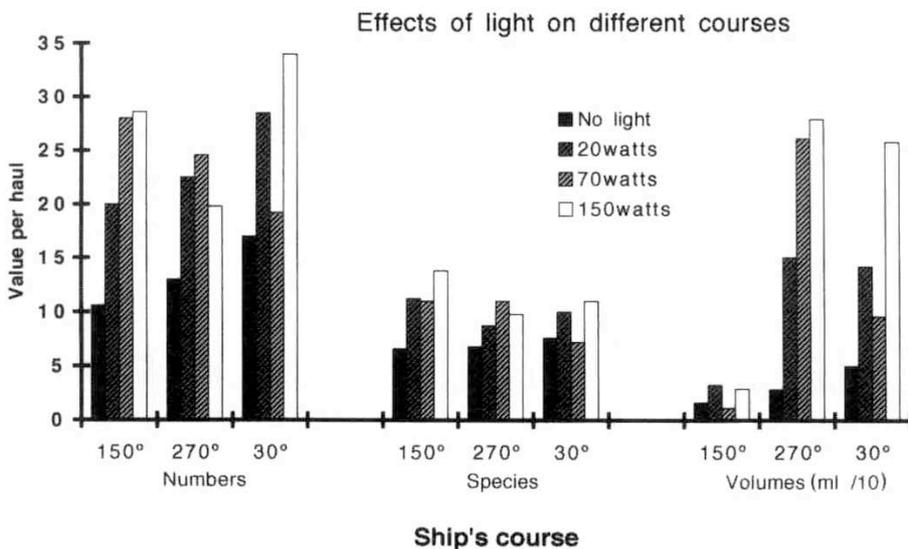
How could capture of squids still be improved? Although RMT had improved the hauls in quality and quantity, with the RMT 90 we had exceeded the size easily handled from a research ship and increases in speed of trawl introduces more damage to the squids.

Sometimes, when a trawl is brought in on a dark night, luminous animals in the water light up the trawl so that the net can be seen from hundreds of meters away, like a ball of blue fire. It may seem remarkable that any squids, with their highly developed eyes, are caught when they can travel fast over several meters and can see a trawl coming at only 2 knots from dozens of meters, possibly 100 m away. It seemed impossible to hide this luminescent light, but what if it attracts squids? If the light were brighter, would it attract more squids? We did trials to test if a diver's light directed forwards from the top bar would affect the catch. Quite dramatically, the results showed that a 70watt light increased the squid and the fish catch by a factor of two by numbers, by volume and by maximum length (Figs 6-8. Clarke & Pascoe 1998). This could be an increase in attraction but it could also be because a bright spotlight may blind them while a diffuse light attracts or merely scares them.

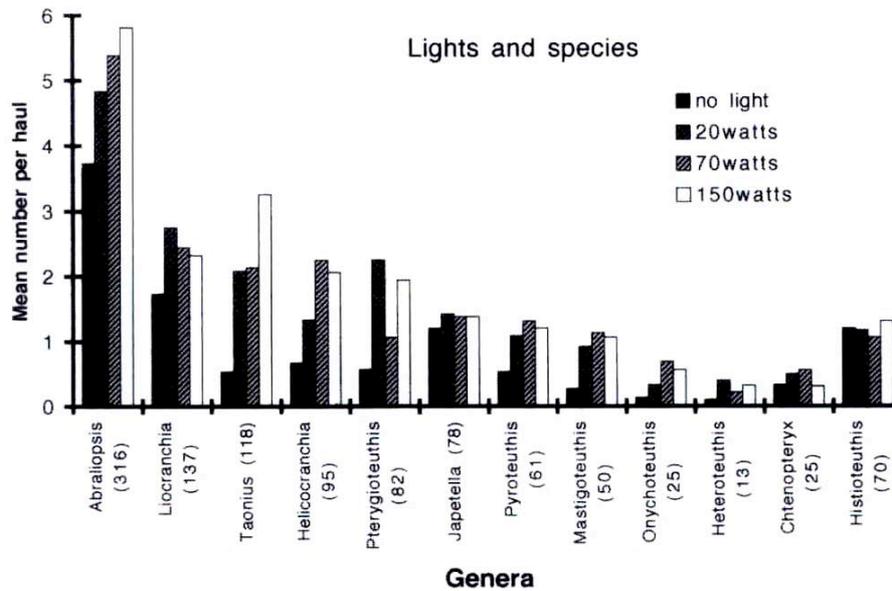
Hundreds of trials taught me that direction of tow relative to the water current influences the catch, the bigger the net the bigger the influence particularly with



**Fig. 6 A**, Effect of light of different powers on total numbers, number of species and volume of largest cephalopods caught by an RMT 50. **B**, Samples split into day and night hauls



**Fig. 7** Effect of trawling direction and light of different powers on numbers of cephalopods caught by an RMT



**Fig. 8** Effect of light of different powers on numbers caught of different cephalopod genera

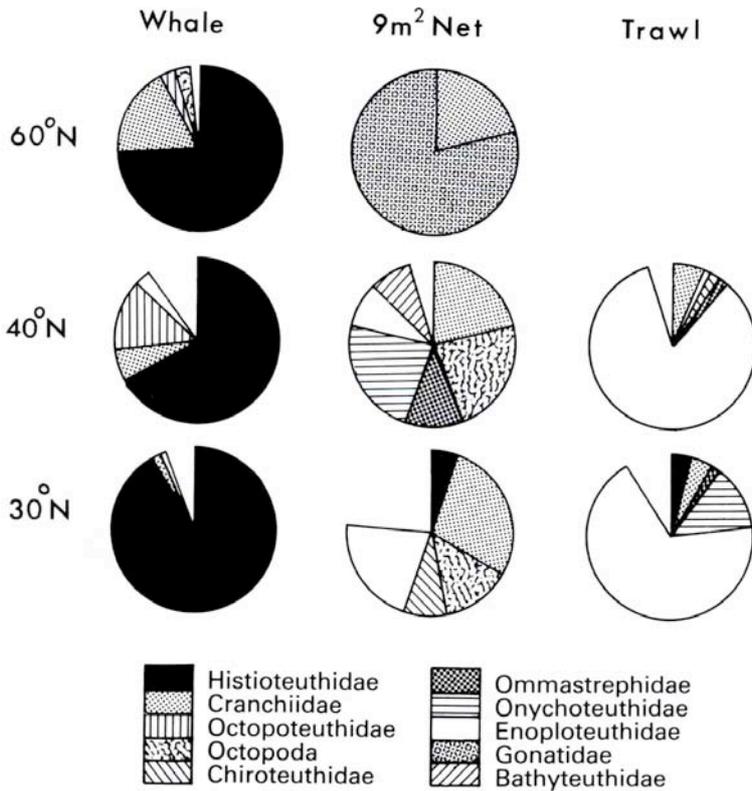
otter trawls. In deep sampling we often have little idea of the relative movement of the water between the surface and the depth sampled. The author found that this could only be taken account of, in comparisons, by sampling the three legs of a triangle and only comparing the same legs with one another (Clarke & Pascoe 1998). Any change in gear or in the operation of the gear, or in the change of the ship can make even comparisons misleading. We may well ask, can we ever obtain a correct measure of what is in the sea or the relative numbers or mass of different organisms without drying it out and seeing what is left? The answer is clearly no! However, net hauls can show vertical distribution and migration and even annual change but only if great care and very considerable expenditure and effort are exercised.

### **Predator studies**

In 1955, three years before joining the N.I.O, the author served a season aboard a whaling factory ship in the Antarctic as a government whaling inspector. Hundreds of sperm whales were examined and notes were made on many anatomical features including their food. While, at that time, the author had no particular interest in squids, he could hardly ignore the large squids, many of which were over one meter and some even three meters in length, or the large numbers of squid jaws in the stomachs. After joining the N.I.O., memories of such large squids and the large numbers

of beaks, which all must have come from larger squids than we were catching in nets, spurred the author to look further into sperm whales stomachs. His first chance came in 1959 when at a whaling station in Madeira he found, in one whale, a bonanza of large and very poorly known squids (Clarke 1962). These included the first heads of the scaled squid *Lepidoteuthis grimaldii*, the first complete *Taningia danae* DML (dorsal mantle length) 140 cm, the first male and the smallest *Architeuthis* DML 38.5 cm, over twenty *Histioteuthis* adults and 2136 lower beaks of these and six other species. Clearly, if the beaks could be identified much more could be learned about the larger species, their numbers and something of their relative importance to the sperm whale. Further, by finding the relationship between the beak length and the body weight, the squid's usual and maximum size and their relative mass in the diet could be calculated.

To fully exploit this observation, the author then set to work learning to identify lower beaks. This proved of particular interest in the case of the sperm whale since calculations from their estimated numbers showed that they consumed, each year, much more than the weight of all marine products removed from the sea by man (>93 million tonnes). This showed that the commoner species in the diet, such as *Histioteuthis*, are very much more numerous and important in the food webs of the deep ocean than was hitherto envisaged. It also showed that the whale was sampling very different species and a very different size range



**Fig. 9** Numbers in the families of squids from nets compared with those in the diet of sperm whales at three latitudes in the North Atlantic

from even the largest nets (Figs 9-11). The author started looking for beaks in more sperm whales, in other cetaceans, in birds, in seals, in fish and even in turtles (e.g. Clarke 1980, 1996, Clarke *et al.* 1981, 1993, Santos *et al.* 2001). Because adults of many of the species were poorly, if at all, represented in net samples, it took many years to relate beak length to body length and mass and this process is still underway (Clarke 1980, 1986a, also see website: [www.cephbase.utmb.edu](http://www.cephbase.utmb.edu)).

Such work has shown us much about the variety of species consumed, from the smallest eaten by small fish and birds to the largest we know from the sperm whale (Fig. 9) including their distribution, relative numbers and mass; every predator species samples differently and provides a different window into the deep sea environment. Providing we have estimates of predator stocks, they can show us how particular predators such as cetaceans or birds may compete with fisheries and how reduction of squid stocks by fisheries may reduce bird, seal and cetacean populations. To monitor the local and global effects of environmental change would be extremely expensive with nets and ships. A much cheaper way to monitor change would be to establish the existing food of a large variety of predators and then look for changes in the diet at

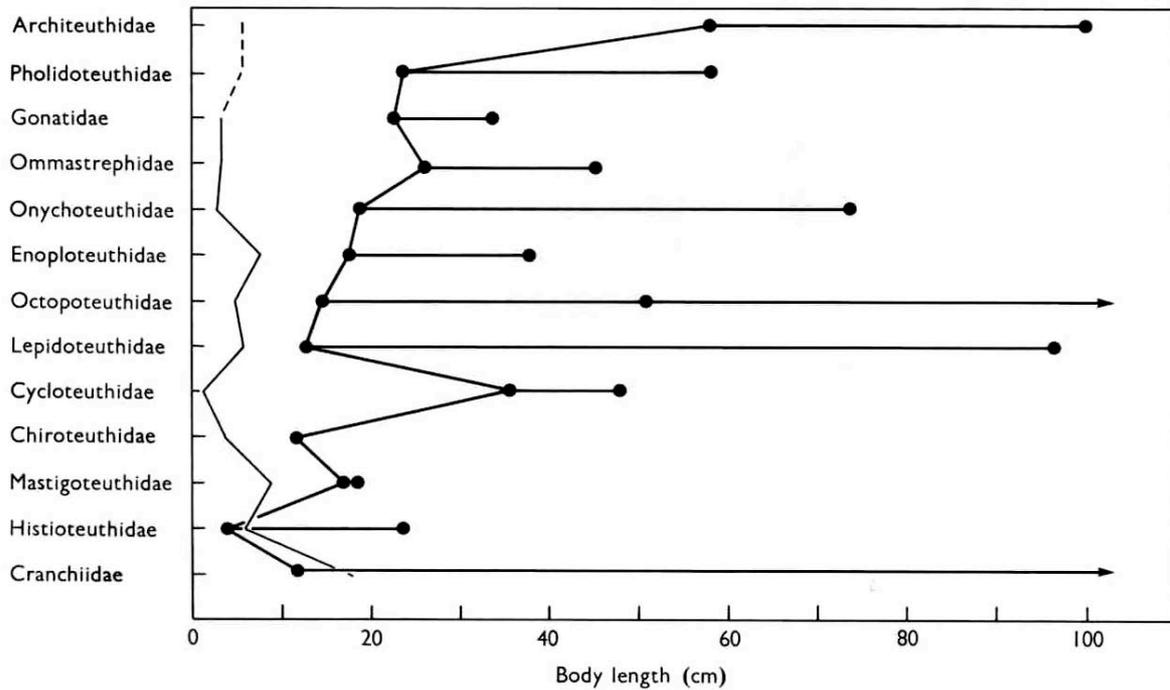
regular intervals. Stomach contents can often be extracted from fish markets or, harmlessly, from nesting birds and seals at little cost compared to running a research ship for net sampling.

In the 1950's, Belyaev found that grabs and dredges used on the bottom of the deep sea sometimes provided large numbers of beaks. He found numbers could reach many thousands per square meter off Arabia and he related numbers to productivity. The author searched through other peoples' collections from the Indian Ocean and did his own grabbing and dredging in the north east Atlantic but none were sufficiently intact to be named.

### **Fossils**

Very few beaks seem to exist as fossils and those seen by the author were squashed beyond recognition.

However, in the squids taken from the Madeira whale, the author first found aragonitic statoliths and they were subsequently found in all squids and their growth rings later became important in the ageing of squids. For years, the author asked geologists and palaeontologists if they had seen such minute stones in fossil deposits but it was only when he met John Fitch of Californian Fish and Game that they were finally



**Fig. 10** Comparison between the maximum mantle lengths of squids of various families caught in nets with those found complete in sperm whale stomachs (Clarke 1977)

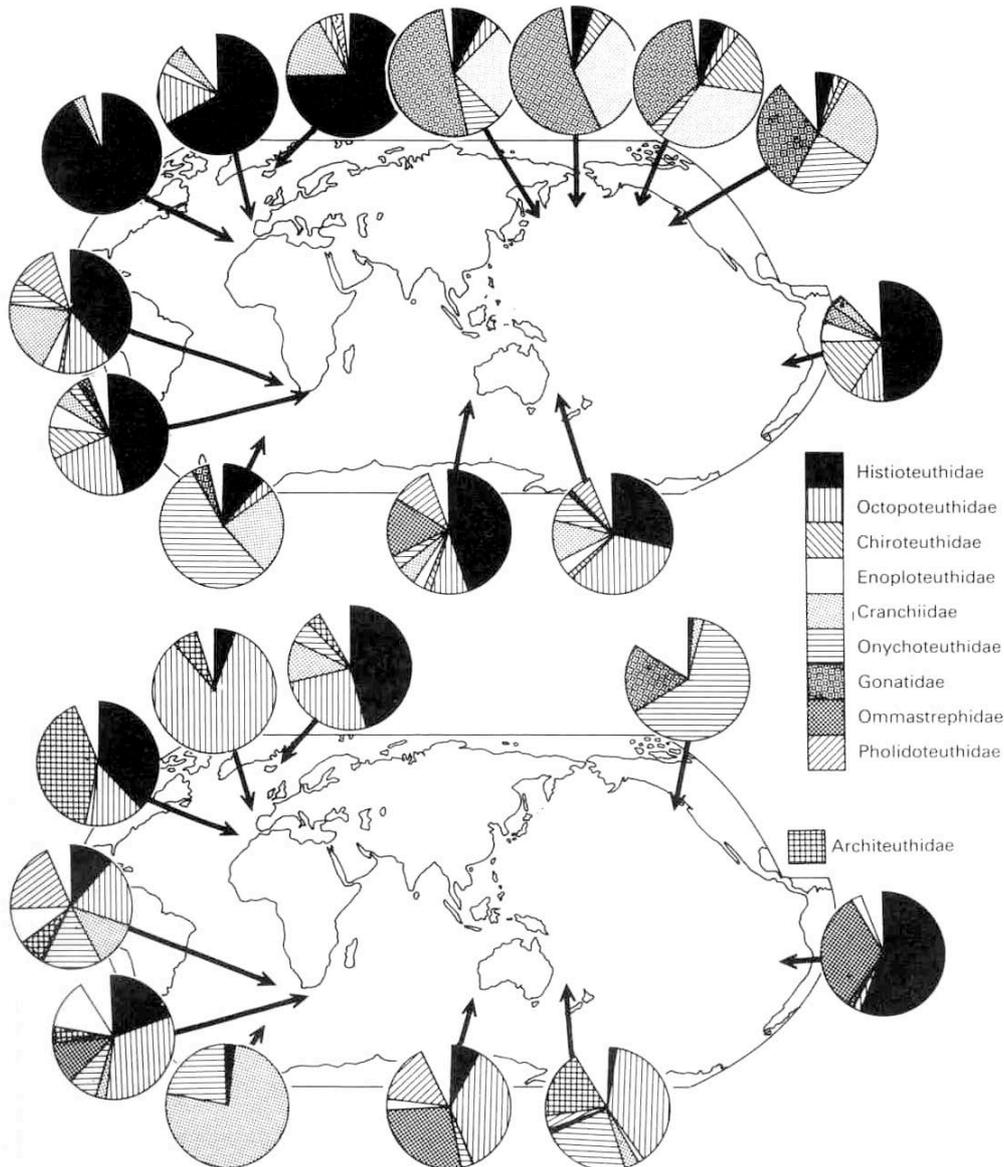
discovered. John was a fanatical siever of ‘dirt’ for fossil fish otoliths and, in his collections, he had a group labelled “?lapilli” which proved, upon examination to be coleoid statoliths very similar to those from living squids. This discovery led us into further searches and comparisons between N. American and European fossils and some from the Pliocene, proved to be from the deep sea genera *Dosidicus*, *Symplectoteuthis* (= *Sthenoteuthis*) and *Moroteuthis* (Clarke & Fitch 1979).

### Hunts for Sea Monsters

In the last few years the media have become attracted to filming giant squids because they are large, have not yet been filmed alive in their natural habitat and have waving tentacles, worthy of anything the name ‘monster’ should have. The author helped Clyde Roper on two National Geographic (films) expeditions. The first, off the Azores, involved attachment of a video camera (‘crittercam’) on the head of sperm whales in the hope that squids attacked by the whales would be filmed. Although the chance of seeing a giant squid was perhaps over-optimistic, since only 0.5 % of squids eaten off the Azores are *Architeuthis* (Clarke *et al.* 1993), we did have hopes that we would film other interesting species such as *Histioteuthis* and *Taningia*.

Unfortunately, the camera was placed a little too far back from the mouth and had not the acuity or light to show enough details of passing particles to identify squid. On a second trip to New Zealand we had the use of an extremely clever R.O.V. designed at M.I.T. with a crittercam attached. However, the Kaikora Canyon, where sperm whales dive, did not yield any squid from midwater or near the bottom. Similarly, extensive video trials in midwater and near the bottom made by a simultaneously run expedition by the National Geographic (Journal) obtained many hours of fish and only a single squid, and that of *Nototodarus*, of little interest to us. My conclusion was that Kaikora Canyon was probably too full of detritus for ‘clean living’ oceanic squids to ever go there and possibly the whales are only eating fish in that area.

The author also helped Steve O’Shea and C.C.Lu during another expedition off New Zealand, run on behalf of the ‘Discovery Channel’. The aim was to find, catch and maintain paralarvae of *Architeuthis*. On one visit, a search through museum collections yielded at least one, possibly two paralarvae under 1cm in length. This was followed by a sea cruise using a RMT50, specially designed for the ship by the author. Very many squids in beautiful condition were collected, including *Architeuthis* paralarvae, but attempts to keep them alive failed.



**Fig. 11** Families of cephalopods found in sperm whale diet showing their importance by number (top) and by estimated mass (bottom)

## DISCUSSION

While the above describes a wide range of efforts to catch and observe oceanic squids the search is not all embracing. In particular, the author has never dived in a submersible and many observations and captures of individual squid have been made by other workers. These and ROVs, used persistently as by the Monterey Institute, are certainly providing much information on behaviour and depth distribution. However, it still seems a mystery why so few squids are seen when sperm whales alone eat > 100 million tonnes of oceanic squid a year, much more than the weight of all fish products caught by man (<96 mt). Our inadequacy may, in part, be due to our inadequacy in fishing within

canyons where sperm whales eat squid or, possibly, lights attached to cameras scare most species away so they cannot be filmed. Or, there again, we may be using the wrong lights on a camera, or the light may have to be bright and moving towards them to effectively increase their observation in the same way as lights on a trawl increase their capture.

Clearly more squids can be caught by increasing the speed of the trawls used but this results in more damage. More can also be caught with increase in the size of the net mouth but limitations are imposed by size and power of the ship. Large oceanic trawlers with the largest midwater trawls now available will certainly increase oceanic squid catches but these are difficult to use in canyons and still may not catch the same species

as whales. Many years fishing with a diversity of nets, a few miles South of Madeira, only once provided a *Histioteuthis bonnellii* although this was the most numerous species in the food of a whale caught off Madeira. Although we can study vertical distribution and migration of small species and paralarvae with RMT, we cannot do this for adults of most species.

If we know squid species are present in an area we might well expect to find vast numbers of their paralarvae. To judge from the condition of the adults in sperm whale stomachs, spawning probably takes place on the sea bottom. Absence of spawn from innumerable bottom trawls carried out by colleagues on the North Atlantic abyssal plain suggests that this must also be in steep sided canyons, inaccessible to trawls. However, we would still expect to catch the paralarvae. As they seem few in midwater and at the surface are they close to the sea bottom?

Sea birds also provide an interesting window into the oceanic squid world. Many include squid species in their diet which nets show to live at considerable depths below the surface; such things as *Chiroteuthis*, *Mastigoteuthis* and *Histioteuthis* (Clarke *et al.* 1981). Is this because current- or wind-induced upwellings in the water bring them near the surface, perhaps for only brief periods? Such local, brief upwellings are extremely difficult to study but may make many species accessible to the birds.

Are all our sampling devices and methods of handling so bad that we must always rely on predators to adequately find what we know to be there?

## ACKNOWLEDGEMENTS

The author would like to very warmly thank all his colleagues who have contributed to this work and been understanding co-authors over many years.

## SELECTED REFERENCES

Baker Ade C, Clarke MR, Harris MJ (1973) The N.I.O. combination net (RMT 1+8) and further developments of rectangular midwater trawls. *J mar biol Ass U K* 53: 167-184

- Clarke MR (1962) Stomach contents of a sperm whale caught off Madeira in 1959. *Norsk Hvalfangst-Tidende* 5: 173-191
- Clarke MR (1969) A new midwater trawl for sampling discrete depth horizons. *J mar biol Ass U K* 49: 945-960
- Clarke MR (1977) Beaks, nets and numbers. *Symp Zool Soc Lond* 38: 89-126
- Clarke MR (1980) Cephalopoda in the diet of sperm whales of the southern hemisphere and their bearing on sperm whale biology. *Disc Rep* 37: 1-324
- Clarke MR (1986a) Handbook for the Identification of Cephalopod Beaks. Oxford University Press
- Clarke MR (1986b) Cephalopods in the diet of odontocetes. In: Bryden MM, Harrison R (eds) *Research on Dolphins*. Oxford University Press
- Clarke MR (1996) Cephalopods as prey. III. Cetaceans. In: Clarke MR (ed.) *The role of cephalopods in the World's oceans*. *Phil Trans R Soc Lond B Spec Vol*, 351: 1053-1065
- Clarke MR, Croxall JP, Prince PA (1981) Cephalopod remains in regurgitations of the wandering albatross *Diomedea exulans* L at South Georgia. *Brit Antarct Surv Bull* 54: 9-21
- Clarke MR, Fitch JE (1979) Statoliths of Cenozoic teuthoid cephalopods from North America. *Palaeontology* 22: 479-511
- Clarke MR, Martins H, Pascoe PL (1993) The diet of sperm whales (*Physeter macrocephalus* Linnaeus 1758) off the Azores. *Phil Trans R Soc Lond B* 339: 67-82
- Clarke MR, Pascoe PL (1998) The influence of an electric light on the capture of oceanic cephalopods by a midwater trawl. *J mar biol Ass U K* 78: 561-575
- Lu CC, Clarke MR (1975) Vertical distribution of cephalopods at 11° N 20°W in the North Atlantic. *J mar biol Ass U K* 55: 369-389
- Santos MB, Clarke MR, Pierce GJ (2001) Assessing the importance of cephalopods in the diets of marine mammals and other top predators: problems and solutions. *Fish Res* 52: 121-139