

**CEPHALOPOD FISHERIES: A FUTURE GLOBAL UPSIDE TO PAST
OVEREXPLOITATION OF LIVING MARINE RESOURCES? RESULTS OF
AN INTERNATIONAL WORKSHOP, 31 AUGUST – 2 SEPTEMBER 1997,
CAPE TOWN, SOUTH AFRICA**

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Management strategies for cephalopod fisheries present similar challenges to those encountered in fisheries for finfish. Peculiarities of cephalopod life cycles and the fact that cephalopod fisheries can benefit from management experiences gained in other fisheries may help to preclude mistakes and management failures. During a three-day workshop, features of cephalopod biology, recommended areas of research and key conclusions for management were identified and points of differences between cephalopods and fish were highlighted. Among these, life-cycle understanding, spatial distribution, stock-recruitment relationship and age determination/growth studies were identified as key priorities for research. Physiological and genetic approaches to understanding basic aspects of the life cycle, and their importance for understanding population dynamics, were stressed. Similarly, theoretical ecology has a role to play in management, e.g. the role of a spatial distribution strategy in survival. Environmental studies are also emerging as being important in the possible prediction of population trends through links that operate at the level of spawning biology. In the interim, cephalopods can be managed using similar principles to those applied to short-lived fish species. Among these, constant proportion harvest strategies were identified as the most effective.

Recently, several critical accounts of marine fisheries management have been published (e.g. Roberts 1997, Rose 1997, Pauly *et al.* 1998). In them, the authors agreed that successes were limited and that, in general, fisheries management has a poor record of sustainable utilization. Indeed, the observation was made that, on a global scale, human exploitation proceeds more or less involuntarily down the trophic pyramid, and the more sought-after species are being replaced by less valuable, smaller ones that grow more quickly.

Fishing for cephalopods is not new, but large-scale commercial fisheries developed only in the 1950s and 1960s. Since then, production and demand have increased steadily and cephalopod fisheries have begun to dominate on some fishing grounds. Therefore, it may be

useful to draw lessons from past finfish exploitation, and thereby to try to avoid similar possible disasters in the field of cephalopod exploitation. To do this, it is considered worthwhile to look at the current status of cephalopod fisheries and at existing data and management options.

These were the aims of a workshop, held at the South African Museum in Cape Town (31 August – 2 September 1997), during which more than 70 participants from at least 20 countries, most of them biologists but also some mathematicians and modellers, shared their experiences and ideas about cephalopod biology and exploitation. The industry was represented by the President of SASMIA (the South African Squid Management Industrial Association).

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Table I: F.A.O. catch statistics, 1993–1995, and an evaluation of whether a taxon was covered during the Cape Town workshop

Taxon	Catch (tons)			Region	Representative coverage?
	1993	1994	1995		
Sepioidea	229 662	239 001	242 079	All	No
<i>Octopus</i> spp.	4 799	8 397	4 191	Senegal	Yes
Octopoda	318 200	287 721	317 706	All except Senegal	No
<i>Loligo gahi</i>	5 305	5 859	22 325	Falklands	Yes
<i>Loligo pealei</i>	22 200	22 502	18 926	NW Atlantic	Yes
<i>Loligo vulgaris reynaudii</i>	6 271	5 814	7 047	South Africa	Yes
<i>Loligo</i> spp.	253 533	236 928	219 827	All (Thailand's share: ~30%)	Yes
<i>Illex illecebrosus</i>	26 353	31 327	19 072	NW Atlantic	Yes
<i>Illex argentinus</i>	330 300	310 075	310 000	SW Atlantic	Yes
<i>Dosidicus gigas</i>	122 431	194 631	99 773	E Pacific	No
<i>Todarodes sagittatus</i>	6 862	6 145	5 273	NE Atlantic	Yes
<i>Todarodes pacificus</i>	548 365	504 408	513 407	NW Pacific	Yes
<i>Nototodarus sloanii</i>	35 060	65 019	71 967	New Zealand	No
<i>Martialia hyadesi</i>	1 252	392	23 868	Falklands	Yes
Squid n.e.i.	736 507	759 638	857 188	All (Falklands ~ 30%, NW Pacific ~ 45%)	Yes
Cephalopods n.e.i.	74 539	98 376	108 411	All (mainly India, 85%)	No
All cephalopods	2 721 639	2 776 233	2 841 060	All	~30% not discussed during workshop

n.e.i. = F.A.O. indication for groupings not indicated to lower taxon

THE WORKSHOP

Structure

The first day of the workshop was devoted to presentations of various examples of cephalopod exploitation worldwide and to approaches to their management. The different fisheries considered are listed in Table I.

The second day was devoted to two major discussion sessions: "Taking stock of finfish fisheries wisdom" (Chair: D. Pauly) and "Taking stock: a different perspective" (Chair: R. K. O'Dor). The discussions highlighted the relevant similarities and differences between fish and cephalopods with respect to resource management.

After the two sessions, discussions continued within a small selected panel, finishing only the following day. During the last day, workshop participants were requested to answer a questionnaire, in which six priority problems in each of three key topics in fisheries science pertaining to cephalopod management had to be identified from lists prepared during earlier plenary discussions.

Selective summary of talks and discussions

Presentations of examples of various cephalopod

fisheries during the workshop encompassed several different approaches to management (see below). All but two suggested that the measures adopted had been successful as far as sustainable utilization of the resources was concerned. Moreover, the two widely known squid fisheries "failures", involving *Todarodes pacificus* (NW Pacific) in the 1970s and *Illex illecebrosus* (NW Atlantic) in the 1980s, appeared to have occurred mainly as a consequence of life-cycle responses to environmental changes, probably aggravated by heavy fishing pressure (Dawe and Warren 1993). Proof of this has been in the recovery of the *T. pacificus* resource, achieved naturally, and not as a result of a long-term change in fishing pressure, management or demand (Sakurai *et al.* 1997, pers. comm.).

Nevertheless, even if the stability in many of the fisheries suggests a sustainable level of utilization, it does not follow that the fishery is necessarily well managed because, for example, the resources in question could be substantially underutilized. Sound fisheries management requires an appropriate balance between the conflicting objectives of maximizing catch and minimizing the risk of unintended severe depletion of the resource. Exactly where the best trade-offs between these two concerns lie for cephalopod fisheries is regrettably not yet clear. However, a reasonable balance between the two in the USA's management strategy for two squid species in the NW Atlantic was noted. Such management is based on a level of total allowable catch that cannot be exceeded

and on an overfishing definition that has been characterized as “risky” (Brodziak and Macy 1996).

The Falkland Islands Government’s management of cephalopod resources appears to be an effective, orthodox approach to large-scale squid fisheries, involving a substantial fleet of large vessels (Beddington *et al.* 1990, Basson *et al.* 1996). A proportional escapement strategy is applied and the basic management tool is control of effort. The control mechanisms used are: 1) limitation on the number of vessels at the beginning of the season; 2) limiting the length of the fishing season (Basson *et al.* 1996). As part of the fishing licence requirement there, each vessel supplies daily all the necessary information required for this approach to be effective. However, such requirements could not easily be set for small-scale fisheries, for which real-time monitoring is impossible.

The management of the chokka squid *Loligo vulgaris reynaudii* fishery in South African waters is an example of the gradual development of some practical variants of effort control, in line with an accumulation of knowledge about the species’ life cycle (Augustyn *et al.* 1994). It is a small-business fishery, involving about 240 boats, ranging between 4 and 15 m long. Although the number of permits issued has been kept constant, effort has been increasing over time. Attempts to limit effort include the imposition of a closed season of variable duration (3–5 weeks) during the peak spawning season, and by the establishment of a marine protected area where fishing is banned.

The primary objective in the management of the Japanese squid fisheries is to obtain good within-season predictions of recruitment as an aid to conducting industrial operations. This is done by early monitoring of environmental conditions, as well as by conducting surveys of paralarvae and pre-recruits (e.g. Murata 1989).

With regard to general problems relevant to all cephalopod fisheries, the applicability of data and ideas from the fields of genetics, physiology, ecology and physical oceanography were discussed. During the discussions, possible differences and similarities between fish and cephalopods were emphasized.

Genetics may be valuable in at least five spheres of fisheries biology:

- taxonomic problems;
- stock structure;
- migration patterns;
- behavioural patterns during spawning;
- monitoring of the level of genetic variability.

While the benefits and application of the first three aspects are fairly obvious, the last two require more clarification. Behavioural patterns during spawning suggest that sperm of at least two categories of males is

used for fertilization. Solution to this paternity problem (Shaw and Boyle 1997) may help to discriminate between demes and/or stocks. From a short-term management perspective, monitoring of the level of genetic variability is probably of little relevance. In the long-term, however, it may affect the ability of the metapopulation (*sensu* McQuinn 1997) to maintain its abundance, or its capability to recover after a crash. Specially interesting is the role of genetic studies in assessing the effectiveness of the “safety valves” – the parts of the metapopulation (such as that in reserves) sheltered by fishing regulations from exploitation. Do they have the potential to rebuild local populations in the event of a crash? This is not a question that can be addressed solely by stock identity and distribution studies.

Physiology often appears to be a theoretical subject, somewhat removed from fisheries science. Discussion at the workshop indicated arguments to the contrary. If an approach based on detailed models of all stages of the life cycle is to become the basis for the management of resource exploitation within the foreseeable future, basic physiological research will be necessary to ascertain the key mechanisms governing the extent and variation of the surplus production capability of the resource each year (e.g. Murphy *et al.* 1994, Wells and Clarke 1996). Energy-transmission modes in cephalopods differ from those of fish in that they are much more oxygen-limited. To overcome this problem they absorb oxygen through their skin; furthermore, their anaerobic metabolism goes through the octopine (and not lactate) chain. Therefore, growth and longevity of squid cannot be understood without basic physiological reviews and research (Jackson 1994, Pauly 1998). During the workshop discussions, consensus was reached on certain points:

- Models required to describe growth of squid may be complex; it is impossible at present to propose a unitary growth model for all cephalopods. It is definitely hazardous to base conclusions about squid growth and longevity only upon unverified field length or mass frequencies. Models fitted on the basis of such data were shown to be questionable when verified with validated statolith age data.
- Schnute’s growth model (Schnute 1981) may be useful if the issue is to distinguish between asymptotic and non-asymptotic growth; many, if not most, cephalopods stop growing or at least slow down during the spawning period. Furthermore, the development of a model which allows for in-season fluctuations in size of cephalopods is a high priority.
- There is a need to revisit the longevity issue for large species of squid; aquarium- and field-validation

experiments on adults of these species should be attempted where possible.

- Small species of squid reach maturity/adulthood within a year or less; because of this, they can generally withstand more intensive fishing pressure. A cautious approach to the exploitation of larger species of squid is advised until fundamental questions relating to growth, age and longevity are resolved.

Theoretical ecology also has a contribution to make in the future management of cephalopod resources. In this regard, the following points were made during the workshop:

- Cephalopods are highly individualistic both with regard to biological parameters (e.g. food consumption, growth) and population ecology (behaviour-related ranking within a local population [deme], demes forming one metapopulation, etc.). The fact that growth rates and their variability may differ between demes means that, unless a random sample of the whole metapopulation can be achieved, age sampling and analyses should be stratified by demes when estimating the metapopulation age structure. The same applies to results of abundance surveys and fisheries statistics as measures of abundance.
- Fish populations have a buffer against interannual recruitment fluctuations provided by the presence of a number of year-classes in the spawning biomass. In contrast, cephalopods often have only one year-class spawning, and hence make extensive use of spatial distribution strategies to enhance survival and so to provide an alternative form of buffer (see Ranta *et al.* 1997 for a theoretical background, and Lipiński 1998 and O'Dor 1998 for cephalopod applications). Spatial and temporal differences in survival of paralarvae and individual somatic growth, as well as distribution, increase variability in the age and size of individuals, and in the numbers in the metapopulation from year to year.
- Because of this spatial aspect of survival, carefully planned and flexible sets of closed areas and times may be used effectively as management tools in most cephalopod fisheries. They should, however, be based on a thorough understanding of the life cycle of the species and, if possible, good biomass estimates.
- A long paralarval/juvenile phase, exponential growth until adulthood, one-year life cycle (in most cases), semelparity, spatial survival strategy, magnitude of differences between individuals, etc., make cephalopods different from fish. These factors are likely to influence the practical aspects of fish-

eries research. Examples are design and interpretation of the results of monitoring programmes, design of assessment models, and choice between management strategies.

In terms of environmental research, the results of which were presented at the workshop mainly by Japanese and South African scientists, the main emphasis was placed on prediction of recruitment. It was pointed out that *T. pacificus* recruitment was related mainly to the area of the spawning grounds: during the 1970s, cooling of the waters above those grounds resulted in decreased spawning activity and lessened recruitment. The recent increase in recruitment is related to warming of the waters north of the "traditional" spawning grounds. In the case of the South African chokka jig fishery, the large monthly and annual catch fluctuations experienced led to uncertainty, and impacted upon resource management, fishery economics and fishers' livelihoods. In 1994, a specific multi-disciplinary research programme was initiated by Sea Fisheries, Cape Town (South Africa). The primary purpose of the initiative was to develop a predictive capability for both chokka recruitment and availability to the fishery. Research at present is focusing on the spawning grounds where the fishery operates, and it is attempting to link regional climatic variability with regional oceanography and global phenomena such as *El Niño* Southern Oscillation (ENSO) events. The work has led to the formulation of models which attempt to couple physical (e.g. temperature and turbidity) and biological (e.g. spawning biology) parameters (Roberts 1998).

Results of the questionnaire

During the third day, the participants of the workshop were requested to define, select and prioritize any six key problems (i.e. simply list them in order of importance) within each of three topics in fisheries science as applied to cephalopods. The three topics were:

- Most important features of cephalopod fisheries biology, as outlined by the Workshop (a list of 10 "problems" had been compiled from which to choose);
- Key areas of research with regard to cephalopods in fisheries science (a list of 29 "problems" had been compiled);
- Main conclusions (of the Workshop) regarding the management of cephalopod utilization (a list of 15 "problems" had been compiled).

More than 70 questionnaires were distributed, and

Table II: Results of the questionnaire on the final day of the Cape Town workshop

Topics and "problems"	Number of respondents assigning the ranking of importance below to the "problem" listed					
	1	2	3	4	5	6
Key features of fisheries biology						
1. Most exploited squid species have a very short lifespan (annual or sub-annual); therefore, the only manner by which catch levels in one year affect abundance in the next is through the stock-recruit relationship	19	5	2	1	0	0
2. Because of the annual nature of squid species and their high level of interannual recruitment variability, constant TAC harvesting strategies involve a relatively low level of resource utilization, although the lack of utilization of good recruitment in certain years of a mid-trophic level species may have ecosystem advantage	2	8	6	5	2	0
3. High within-season variability linked to pulse recruitment						
4. Improved management measures would likely result from real-time monitoring	2	4	2	5	4	3
5. Short duration of adult phase in relation to total lifespan	2	2	5	0	4	3
	1	2	6	6	2	2
Key areas of research						
1. Clarify the life cycle in space and time (e.g. duration of different stages, location of spawning, nursery, feeding grounds)	13	6	4	2	2	0
2. Identify links between the environment and resource recruitment	4	5	1	4	3	1
3. Systematics (including paralarvae)	3	1	0	1	1	1
4. Stock structure (genetics), good idea of stock differentiation for management	2	4	2	0	2	1
Key conclusions regarding management						
1. Account needs to be taken in assessments that squid recruitment at the fishing grounds occurs as a series rather than as a single pulse	5	5	3	4	2	1
2. The optimal approach to management depends upon objectives which may vary for different fisheries; one cannot maximize catches and minimize catch variability – there is a need for trade-offs (risk, policy)	5	2	2	2	0	2
3. Because information on cephalopod fisheries is relatively sparse relative to the situation in finfish, more benefit can be expected of research in this area	4	1	1	0	1	3
4. Effort control is a cheaper alternative than TAC, but account needs to be taken of the possibilities that <i>cpue</i> is not proportional to overall abundance, and of increased efficiency	3	2	5	2	1	0

TAC = Total Allowable Catch

33 were returned, the collective results of which are given in Table II. It is apparent that, although strong and varying views were expressed, a fairly high level of consensus was reached regarding key features of cephalopod fisheries biology and research. The key conclusions regarding management of cephalopods were less clear.

In terms of the key features of cephalopod fisheries biology, the most commonly endorsed view was that "most exploited squid species have a very short lifespan (annual or sub-annual); therefore, the only manner by which catch levels in one year affect abundance in the next is through the stock-recruit relationship". This opinion underlines the importance of what are currently the most crucial problems in cephalopod assessment, namely longevity, growth and stock-recruit relationships.

For the key areas of cephalopod research, the most commonly accepted need was to "clarify the life cycle in space and time (e.g. duration of different stages, location of spawning, nursery, feeding grounds)". Of second importance was to "identify links between the environment and resource recruitment".

In the key conclusions regarding management of cephalopods, the most frequently chosen statement was that "account needs to be taken in assessments that squid recruitment at the fishing grounds can occur as a series rather than a single pulse". Other important points were, respectively:

- "the optimal approach to management depends upon objectives which may vary for different fisheries; one cannot maximize catches and minimize catch variability – there is a need for trade-offs";

- “because information on cephalopod fisheries is relatively sparse relative to the situation in finfish, more benefit can be expected from research in this area”;
- “effort control is a cheaper alternative than [Total Allowable Catch] TAC, but account needs to be taken of the possibilities that [catch per unit effort] *cpue* is not proportional to overall abundance, and of increased efficiency”.

In this prioritization of important issues in cephalopod management, there is an emergent dualism between finfish-derived, cautious observations and recommendations specific to the squid life cycle. The value of research in correctly shaping cephalopod fisheries, and their management, also scored highly.

HOW TO AVOID MISTAKES OF THE PAST: CONCLUSIONS

It became abundantly clear that the views of most participants were that current research should concentrate on improving understanding of the biology of cephalopods in a life-cycle approach. Spatial variations of cephalopod survival should be taken into account, particularly when extrapolating abundance survey results and fisheries statistics. Spatial variability is also a key factor to consider when selecting areas for, and/or timing of, closures in effort-regulated fisheries. The implementation of a management regime through a limited entry programme needs reasonably good estimates of biomass, which are seldom available. In the absence of such data, a cautious trial-and-error adaptive management approach is required which demands that effort levels are reviewed periodically. Further, effort has to be reduced immediately after a substantial decrease in catch rates.

Differences between fish and squid are likely to be important at the following stages:

- design of monitoring programmes (e.g. temporal and spatial scale of catch and effort data);
- design of assessment models;
- choice of management strategies.

It is therefore of great importance to research to establish these differences. However, cephalopod and finfish fisheries are similar in that both require stable, long-term monitoring in order to understand the dynamics of the resources and the associated fleets. There is no panacea for a lack of long-term monitoring. Where environmental forcing or community-level dynamics have strong effects on resource productivity, they need to be monitored and understood as well.

LITERATURE CITED

- AUGUSTYN, C. J., LIPÍŃSKI, M. R., SAUER, W. H. H., ROBERTS, M. J. and B. A. MITCHELL-INNES 1994 — Chokka squid on the Agulhas Bank: life history and ecology. *S. Afr. J. Sci.* **90**(3): 143–154.
- BASSON, M., BEDDINGTON, J. R., CROMBIE, J. A., HOLDEN, S. J., PURCHASE, L. V. and G. A. TINGLEY 1996 — Assessment and management techniques for migratory annual squid stocks: the *Illex argentinus* fishery in the Southwest Atlantic as an example. *Fish. Res.* **28**(1): 3–27.
- BEDDINGTON, J. R., ROSENBERG, A. A., CROMBIE, J. A. and G. P. KIRKWOOD 1990 — Stock assessment and the provision of management advice for the short fin squid fishery in Falkland Islands waters. *Fish. Res.* **8**: 351–365.
- BRODZIAK, J. K. T. and W. K. MACY 1996 — Growth of long-finned squid, *Loligo pealei*, in the northwest Atlantic. *Fishery Bull., Wash.* **94**(2): 212–236.
- DAWE, E. G. and W. G. WARREN 1993 — Recruitment of short-finned squid in the Northwest Atlantic Ocean and some environmental relationships. *J. Cephalopod Biol.* **2**(2): 1–21.
- JACKSON, G. D. 1994 — Application and future potential of statolith increment analysis in squids and sepioids. *Can. J. Fish. Aquat. Sci.* **51**(11): 2612–2625.
- LIPÍŃSKI, M. R. 1998 — Cephalopod life cycles: patterns and exceptions. In *Cephalopod Biodiversity, Ecology and Evolution*. Payne, A. I. L., Lipiński, M. R., Clarke, M. R. and M. A. C. Roeleveld (Eds). *S. Afr. J. mar. Sci.* **20**: 439–447.
- McQUINN, I. H. 1997 — Metapopulations and the Atlantic herring. *Revs Fish Biol. Fish.* **7**(3): 297–329.
- MURATA, M. 1989 — Population assessment, management and fishery forecasting for the Japanese common squid, *Todarodes pacificus*. In *Marine Invertebrate Fisheries: their Assessment and Management*. Caddy, J. F. (Ed.). New York; Wiley: 613–636.
- MURPHY, E. J., RODHOUSE, P. G. and C. P. NOLAN 1994 — Modelling the selective effects of fishing on reproductive potential and population structure of squid. *ICES J. mar. Sci.* **51**(3): 299–313.
- O’DOR, R. K. 1998 — Can understanding squid life history strategies and recruitment improve management. In *Cephalopod Biodiversity, Ecology and Evolution*. Payne, A. I. L., Lipiński, M. R., Clarke, M. R. and M. A. C. Roeleveld (Eds). *S. Afr. J. mar. Sci.* **20**: 193–206.
- PAULY, D. 1998 — Why squid, though not fish, may be better understood by pretending they are. In *Cephalopod Biodiversity, Ecology and Evolution*. Payne, A. I. L., Lipiński, M. R., Clarke, M. R. and M. A. C. Roeleveld (Eds). *S. Afr. J. mar. Sci.* **20**: 47–58.
- PAULY, D., CHRISTENSEN, V., DALSGAARD, J., FROESE, R. and F. TORRES 1998 — Fishing down marine food webs. *Science* **279**(5352): 860–863.
- RANTA, E., KAITALA, V. and P. LUNDBERG 1997 — The spatial dimension in population fluctuations. *Science* **278**(5343): 1621–1623.
- ROBERTS, C. M. 1997 — Ecological advice for the global fisheries crisis. *Trends Ecol. Evol.* **12**(1): 35–38.
- ROBERTS, M. J. 1998 — The influence of the environment on chokka squid *Loligo vulgaris reynaudii* spawning aggregations: steps towards a quantified model. In *Cephalopod Biodiversity, Ecology and Evolution*. Payne, A. I. L., Lipiński, M. R., Clarke, M. R. and M. A. C. Roeleveld (Eds). *S. Afr. J. mar. Sci.* **20**: 267–284.
- ROSE, G. A. 1997 — The trouble with fisheries science! *Revs Fish Biol. Fish.* **7**(3): 365–370.
- SAKURAI, Y., KIYOFUJI, H. and S. SAITOH 1997 — The effect

- of changing environmental regimes on *Todarodes pacificus* populations: a possible scenario. In *Programmes and Abstracts of CIAC '97. Cephalopod Biodiversity, Ecology and Evolution, Cape Town, August/September 1997*: 80–81.
- SCHNUTE, J. [T.] 1981 — A versatile growth model with statistically stable parameters. *Can. J. Fish. aquat. Sci.* **38**(9): 1128–1140.
- SHAW, P. W. and P. R. BOYLE 1997 — Multiple paternity within the brood of single females of *Loligo forbesi* (Cephalopoda: Loliginidae), demonstrated with microsatellite DNA markers. *Mar. Ecol. Prog. Ser.* **160**: 279–282.
- WELLS, M. J. and A. CLARKE 1996 — Energetics: the costs of living and reproducing for an individual cephalopod. *Phil. Trans. R. Soc. Lond.* **351B**: 1083–1104.