

Chapter 13

Overview

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1 Introduction

Trends in global fisheries show that 1990 marked the first decline in total world catch since 1976 and that for several years there has been a trend of decline in traditional resources accompanied by an increase in exploitation of new species. Many of these new resources are short-lived species, including cephalopods, which have expanded and replaced those depleted by fishing. Although many of the replacement stocks are of lower value, the cephalopods are an exception and the world catch has risen because of large distant-water fleets exploiting stocks, especially of ommastrephids, on the outer shelves and oceanic waters of the southwest Atlantic, northwest Pacific and central eastern Atlantic (FAO 1994). Furthermore, there are as yet unexploited stocks of cephalopods, some in environmentally fragile areas such as the Southern Ocean (Rodhouse 1993), which are likely to come under pressure of exploitation in the near to medium future.

Species of the genus *Illex* remain the most important of the current squid fisheries in terms of catch size. The *Illex* species provide useful models for cephalopod recruitment processes, not only because of their commercial importance but also because, in the case of *Illex illecebrosus*, there is dramatic evidence of the catastrophic effect of recruitment failure on a major stock. Our purpose here is to highlight areas where knowledge of the biology of recruitment, and associated processes, is lacking and try to identify the innovative research needed to address specific problems. Finally we attempt to illustrate how these research areas might come together to comprehensively tackle the question of recruitment variability in squid stocks.

2 Systematics and stock discrimination

The most fundamental problem in any fishery is to understand the taxonomy of the exploited species and to be aware of the degree to which species are subdivided into effective populations or stocks. This requires an understanding of the processes of gene flow from the level where genetic exchange is prevented by reproductive isolation between species to the more subtle problems of stocks that are effectively panctic but where exchange is sufficiently low to warrant discrete management of a fishery.

Although cephalopod systematists are generally satisfied with the current taxonomy of species within the genus *Illex*, questions are raised (*see Chapter 1*) about opportunities for interbreeding, especially but not exclusively, in the North Atlantic. It is fundamental that questions of species identity and genetic distance be tackled by research combining the methods of conventional taxonomy and biochemical and molecular genetics. There is also genetic evidence for high levels of discrimination between samples of *Illex argentinus* with little temporal and spatial separation (Carvalho *et al.* 1989). In another ommastrephid there is evidence for cryptic speciation (Brierley 1993). These preliminary data point to complexities of stock structure, possibly related to school structure, that imply unusual reproductive behaviour at the population level best tackled using the population genetics approach.

3 Early life history

The life cycles of the three exploited species of *Illex* are imperfectly understood. The most profitable area for future research must be on the early phase of the life cycle. Good knowledge of geographical and temporal location of spawning areas and the distribution and transport of eggs and paralarvae would contribute significantly to resolution of problems concerning species distributions, overlaps in range, and the subdivisions into stocks or populations. Furthermore, good descriptive knowledge of the early life stage biology would allow the generation of testable hypotheses about what physical variability in the ocean drives variability in the stocks of the different species.

The most immediate priority is to examine sampling methods and explore possible new technologies. Use of research nets fitted with lights has been shown to improve sampling efficiency for later life stages of several species of oceanic squid (Clarke 1985), and light traps have been effective for trapping paralarval and juvenile stages of neritic squid (Moltschanivskyj and Doherty 1994). Nets and low-cost traps employing light have not been assessed for sampling omnastrophid paralarvae and juveniles in the oceanic environment.

Although in the past paralarval surveys have followed pre-set grid patterns, transects, etc., future sampling should utilize real-time synoptic remote sensing data to identify surface temperature and ocean colour features. Existing data for ommastrophid distributions in relation to the physical environment show that concentrations of squid and their predators are often related to ephemeral features including fronts, warm- and cold-core eddies and streamers (Sugimoto and Tameishi 1992, Waring *et al.* 1993). Considerable progress will be made in future by biological sampling within these features as they develop through time and space.

4 Trophic relations

It is evident that in squid, which grow exceptionally fast and have metabolic rates to match, the imperative to feed voraciously and avoid prolonged fasting is foremost among the factors influencing behaviour of a cohort. From hatching, squid must track concentrations of food species across the features of the physical environment which promote concentration of biological activity. Their fast growth entails rapid shifts between trophic niches. The biomass spectra of pelagic plankton/nekton communities are characterized by peaks and troughs (Boudreau and Dickie 1992) so that as squid feed and grow they must track across the biomass spectrum and each trough creates a critical point in the life cycle.

Following the shifts in diet of a cohort as it migrates and grows, and as it follows the key physical features of the oceanic environment, would reveal the critical points in time and space when trophic ecology contributes to recruitment success. An important part of this research can be approached by sampling from the fishery but there is also a requirement to sample diet during the pre-recruit phase.

Predation on squid, although not given major consideration in this volume, is a major potential source of variability in recruitment success. It is likely to be concentrated at particular points in the life cycle. Once these have been identified the use of beaks in predator stomachs provides a reliable means of assessing the extent of predation on stocks (Clarke 1986) and indeed provides a wealth of information that often cannot be easily obtained from other sources.

5 Growth and maturation

Estimation of cephalopod growth has been a major "growth industry" in cephalopod biology in recent years. Growth estimates obtained" from shifts in cohort size structure and from ageing studies based on the statoliths are liable to be biased where samples are taken from a fishery which exploits a cohort at a point on a migration route (Hatfield and Rodhouse 1994) and because of effects related to Lee's phenomenon (Rodhouse *et al.* 1988). The daily nature of growth increments in the statolith has been established beyond reasonable doubt in several species of omrnastrophid and loliginid squid and has been applied in several growth studies. Preparing and counting statoliths is time-consuming and tedious so the technique is only useful for specific problems requiring relatively small data sets. Large-scale use of statoliths in growth studies will be possible when technology (image analysis, etc.) allows the processes involved to be automated.

The time period of growth increments in the gladius is less well established although several lines of evidence support the one per day hypothesis. Provided experimental work can establish this unequivocally across species, the technique has great potential because of the opportunity it provides of reconstructing individual growth histories.

The ability to reconstruct the environmental histories of individual squid would provide a potentially powerful approach to questions about migrations between water masses, effects of thermal history on growth and maturation as well as discrimination of stocks. Strontium/calcium ratio appears to change systematically along the growth axis in statoliths of the ormnastrophid *Martialia hyadesi* (Rodhouse *et al.* 1994), In fish this has been shown to provide a record of thermal history as the ratio is inversely related to ambient temperature (Radtke 1989), and also of salinity history as the ratio is positively related to this variable (Rieman *et al.*, 1994). However, because of the potential confounding effects of these variables on one another there is a need to for the relationships between different environmental parameters and Sr/Ca ratios to be carefully established experimentally in the squid statolith. The relationship between temperature and oxygen isotope ratios in calcareous structures in marine organisms is better established and has been exploited to validate annual growth increments in sections of bivalve shells (Margosian *et al.*, 1987, Tan *et al.* 1988). Current technology cannot deal with samples as small as would be needed to discriminate oxygen isotope ratios between growth zones on sectioned squid statoliths. However, laser ablation techniques are likely to be applicable on smaller scales in the future. The trace element signature in otoliths has been used to discriminate among fish stocks (Gunn *et al.* 1992) and this approach may complement use of population genetics methods and, indeed, parasite markers in studies of stock discrimination in squid if the methods can be applied to the statolith.

The processes of maturation and spawning in the *Illex* spp. are poorly understood. Potential fecundity has been estimated by counting eggs in the oviduct of mature females, on the assumption that ovarian eggs that have not fully ripened will not be spawned. Counts have been made of vitellogenic eggs in the oviduct aRd ovary together assuming that eggs in the ovary that have not fully developed will ultimately reach full development. Finally counts have been made of all eggs, including pre-vitellogenic, assuming multiple spawnings events between which further vitellogenesis takes place in the ovary (Laptikhovsky and Nigmatullin 1993). Spawning has rarely been observed in the laboratory and never in the field so there are serious gaps of knowledge in this fundamental life-cycle process.

6 Stock assessment

Addressing problems of recruitment variability in short-lived species such as squid requires a different approach, different research skills and different models to those applied to problems with the more conventional long-lived species of commercially exploited fish. One fundamental difference is the need for real-time assessment and monitoring of squid stocks and their environment. The poor relationship between spawning stock and recruitment strength in squid stocks dictates that recruitment cannot be predicted with any precision prior to the appearance of the new recruits in the fishery, or at best only a short time in advance

of recruitment. Retrospective analysis of data is virtually useless for management purposes because at any time the next recruitment event is dependent on the breeding success of the cohort currently under exploitation.

Formal, numerical models used for assessment purposes are only of value if they are based on conceptual models derived from research data that link knowledge of biological factors with knowledge of physical factors. Managers must remain flexible in order to incorporate the results of new research data in their models. It cannot be emphasized too much that the biology of the exploited squid stocks in all cases is poorly understood.

The use of acoustic technology to complement catch-based assessment methods is needed. Use of multifrequency methods to discriminate among targets (Madureira *et al.* 1993) and split-beam transducers to establish in situ individual target strength of different squid species are research areas that are ready for development in the context of squid fisheries.

7 Conclusion

Useful understanding of the processes driving recruitment variability in squid stocks will only be gained by interdisciplinary research that crosses the boundaries of organismal biology, sampling technology, physical oceanography, population genetics and fisheries dynamics. But the most important collaboration will probably be between physical oceanographers who are sensitive to the requirements of fisheries ecology and marine biologists who can communicate their science to the physical oceanography community. Mann and Lazier (1991) have pointed out that much of the variance in marine productivity is a function of water movement. With remote sensing technology providing real-time synoptic information on the physical processes taking place at fronts, in eddies and at shelf breaks, etc. many previously intractable problems of large-scale processes in the biology of pelagic squid are now ready and waiting to be addressed.

The two species that inhabit western boundary currents in the North and South Atlantic, *I. illecebrosus* and *I. argentinus*, in many ways present north/south ecological mirror images of one another. Furthermore, the collapse of the *I. illecebrosus* stock in the early 1980s was rapidly followed by the boom in the *I. argentinus* fishery. These circumstances provide a rare opportunity in marine ecology to apply the comparative approach to problems that may seem intractable viewed in isolation.

References

- BOUDREAU, P.R. & DICKIE, L.M. 1992. Biomass spectra of aquatic ecosystems in relation to fisheries yield. *Can. J. Fish. Aquat. Sci.*, 49: 1528–1538.'
- BRIERLEY, A.S., RODHOUSE, P.G., THORPE, J.P. & CLARKE, M.R. 1993. Genetic evidence of population heterogeneity and cryptic speciation in the ommastrephid squid *Martialia hyadesi* from the Patagonian Shelf and Antarctic Polar Frontal Zone. *Mar. Biol.*, 116: 593–602.
- CARVALHO, G., THOMPSON, A. & STONER, A.L. 1992. Genetic diversity and population differentiation of the shortfin squid *Illex argentinus* in the south-west Atlantic. *J. Exp. Mar. Biol. Ecol.*, 158: 105–121.
- CLARKE, M.R. 1986. *A handbook for the identification of cephalopod beaks*. Oxford, Clarendon Press, 273 pp.
- CLARKE, M.R. & PASCOE, P.L. 1985. The influence of an electric light on the capture of deep-sea animals by a midwater trawl. *J. Mar. Biol. Assoc. UK*, 65: 373–393.
- FAO. 1994. *Review of the state of world fishery resources*. FAO Marine Resources Service, Fishery Resources and Environment Division. FAO Fisheries Technical Paper No. 335. Rome, 136 pp.
- GUNN, J.S., HARROWFIELD, I.R., PROCTOR, G.H. & THRESHER, R.E. 1992. Electron probe microanalysis of fish otoliths - evaluation of techniques for studying age and stock discrimination. *J. Exp. Mar. Biol. Ecol.*, 158: 1–36.
- HATFIELD, E.M.C. & RODHOUSE, P.G. 1994. Migration as a source of bias in the measurement of cephalopod growth. *Antarctic Sci.*, 6: 179–184.
- LAPTIKHOVSKY, V.V. & NIGMA TULLIN, CH. 1993. Egg size, fecundity, and spawning in females of the genus *Illex* (Cephalopoda: Ommastrephidae). *ICES J. Mar. Sci.*, 50: 393–403.
- MADUREIRA, L.S.P., WARD, P. & ATKINSON, A. 1993. Differences in backscattering strength determined at 120 and 38 kHz for three species of Antarctic macrozooplankton. *Mar. Eco. Frog. Ser.*, 93: 17–24.

- MANN, K.H. & LAZIER, L.R.N. 1991. *Dynamics of marine ecosystems*. Boston, Blackwell Scientific Publications, 466 pp.
- MARGOSIAN, A., TAN, F.C., CAI, D. & MANN, K.H. 1987. Seawater temperature records from stable isotope profiles in the shell of *Modiolus modiolus*. *Estuarine Coastal Shelf Sci.*, 25: 81–89.
- MOLTSCHANIWSKYJ, N.A. & DOHERTY, P.J. 1994. Distribution and abundance of two juvenile tropical Photololigo species (Cephalopoda, Loliginidae) in the central Great Barrier Reef lagoon. *Fish. Bull.*, 92: 302–312.
- RADTKE, R.L. 1989. Strontium-calcium concentration in fish otoliths as environmental indicators. *Compo Biochem. Physiol.*, 92A: 189–193.
- RIEMAN, B.E., MYERS, D.L. & NIELSON, R.L. 1994. Use of otolith microchemistry to discriminate *Oncorhynchus nerka* of resident and anadromous status. *Can J. Fish. Aquat. Sci.*, 51: 68–77.
- RODHOUSE, P.G., SWINFEN, R.C. & MURRAY, A.W.A. 1988. Life cycle, demography and reproductive investment in the myopsid squid, *Alloteuthis subulata*. *Mar. Ecol. Prog. Ser.*, 45: 245–253.
- RODHOUSE, P.G., ROBINSON, K., GAJDATSY, S.B., DALY, H.I. & ASHMORE, M.J.S. 1994. Growth, age structure and environmental history in the cephalopod *Martialia hyadesi* (Teuthoidea: Ommastrephidae) at the Antarctic Polar Frontal Zone and on the Patagonian Shelf Edge. *Antarctic Sci.*, 6: 259–267.
- RODHOUSE, P.G., CROXALL, J.P. & PRINCE, P.A. 1993. Towards an assessment of the stock of the ommastrephid squid *Martialia hyadesi* in the Scotia Sea: data from predators. In T. OKUTANI, R.K. O'DOR & T. KUBODERA, eds. *Recent advances in cephalopodfisheries biology*, pp. 433–440. Tokyo, Tokai University Press.
- SUGIMOTO, T. & TAMEISHI, H. 1992. Warm-core rings, streamers and their role on the fishing grounds formation around Japan. *Deep-Sea Res.*, 39 (Suppl.1): S183–S201.
- TAN, F.C., CAI, D. & RODDICK, D.L. 1988. Oxygen isotope studies on sea scallops, *Placopecten magellanicus*, from Browns Bank, Nova Scotia. *Can. J. Fish. Aquat. Sci.*, 45: 1378–1386.
- WARING, G.T., FAIRFIELD, C.P. RIHSAM, C.M. & SAND, M. 1993. Sperm whales associated with Gulf-Stream features off the north-eastern USA shelf. *Fisheries Oceanogr.*, 2: 101–105.

Squid are among the fastest-growing short-lived commercial species, and, as opposed to most finfish resources worldwide, their contribution to the total world fish production has been increasing at a high rate in the past two decades. Since squids tend to have higher global market value than many fish, they have the potential to produce both larger and more valuable catches, given the same level of primary productivity. As annuals, ommastrephid squid, such as those in the genus *Illex* used as an example in this volume, grow rapidly with high production-to-biomass ratios but have no reserves of genetic diversity once a year class is overfished. Thus, detailed understanding of stock structure and highly variable recruitment dynamics is required to ensure conservation of the resource base and to achieve sustainability of directed fisheries. Increment analysis for age and growth and stomach content analysis indicate flexible seasonality and feeding strategies allowing a wide range of habitats. *Illex coindetii* occupies the Mediterranean, Caribbean and eastern Atlantic margin from 55°N to 20°S but never sustains major fisheries. In the western boundary currents of the Atlantic, *Illex illecebrosus* collapsed after intense, widely distributed fishing in the north, while in the south, *Illex argentinus* has survived much longer as the world's largest squid fishery, possibly stabilized by a complex of stocks, with widely dispersed breeding in space and time. Selective gears in feeding areas may be self-limiting, as long as migration ensures adequate escapement and the squid are not pursued into breeding areas. Recruitment appears to be limited by food production and by instabilities in the interactions between adult migrations and ocean physics, which strongly influence early growth and survival. After chapters reviewing the principal commercial *Illex* species, both techniques and results of studies on these influencing factors are reported in separate chapters by experts in their fields.

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