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*
1998

CEPHALOPOD LIFE CYCLES: PATTERNS AND EXCEPTIONS

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A holistic (life-cycle orientated) approach to ecological research and resource management of cephalopods is outlined. The first phase of such an approach involves the collection of basic life-cycle data; the second phase involves developing predictive models of stock response to harvesting that incorporate information on the life history, the third is the implementation of management measures. The crucial data required are those on species distribution (preferably on distribution of species concentrations) and on the basic life cycle itself. The survival strategy of cephalopods is spatially orientated (i.e. how and to what extent individuals are distributed is directly linked to the success or failure of the next generation). The use of basic life-cycle parameters in management application is emphasized, and comparisons in this regard are drawn with the management of teleost stocks.

Cephalopods belong to a very diverse group of animals, comprising relatively large numbers of monotypic (Nesis 1987) and stenotypic (few species) families, a phenomenon probably attributable to their long and dramatic history of radiations and extinctions (Teichert 1988). Superficially, the species composition of the group suggests that it was extinction-driven rather than radiation-driven (Teichert 1988, pp. 70–72). The latter would be typical of a very speciose group of competitors, e.g. fish (Greenwood *et al.* 1979, Hinegardner and Rosen 1979).

Exploitation of cephalopods is on the increase (Clarke 1996a, Beddington 1997, F.A.O. 1997, Pauly *et al.* 1998), partly because some species, and indeed some cephalopod families (e.g. the Loliginidae and the Ommastrephidae), are ecologically highly successful. Their ecological success may be measured by their distribution, numbers, biomass and trophic importance (including importance in local and global fisheries). For more specific definitions and examples, the reader is referred to Lipiński (1992) and Clarke (1996b). Cephalopods are traditionally highly regarded as food for direct human consumption in many countries (Tomiyama and Hibiya 1978). In addition, they continue to be accepted into totally new markets (Lipiński 1977).

To avoid the many pitfalls characteristic of the management of the exploitation of finfish is a challenge for fisheries scientists (Roberts 1997). The tasks facing fisheries scientists are well known (Mangel *et al.* 1996) and may be summarized as follows:

- resources should not collapse as a result of human interference;
- ecosystem coherence should be maintained;
- fisheries should be economically sustainable and profitable;
- knowledge about any resource should be gained in a progressive, non-destructive manner, preferably prior to the resource being adversely impacted.

The problems which managers of any living, natural resource face are also well known and include:

- time-series of catches and other statistics which are short, incomplete and biased;
- data collection which is time- and area-limited, because human and financial resources are badly constrained;
- biological data which are limited, biased or unreliable;
- theoretical models and options which are weakly developed, insufficiently supported, and incorporating parameters that are difficult to estimate and conclusions which are difficult to apply;
- socio-economic and political situations which are complex, making policy decisions prone to pressure from powerful interest groups (lobbies).

Cephalopods are physiologically and ecologically less well known than finfish, largely because of a lack of systematic stability within the group, difficulties in collecting data in the field and, perhaps of lesser applied importance, difficulties until recently in keeping cephalopods in aquaria, despite enthusiastic research attempts in recent years. Can the resource management challenges be met under such difficult circumstances? Certainly, there is a conceptual background to be drawn upon from finfish experience (Langton *et al.* 1995). Those authors stress that only ecosystem- and life-cycle-orientated research on multi-spatial and multi-temporal scales can address successfully all the management tasks outlined above. A good example in this regard in the field of cephalopod exploitation has been set by the Japanese approach to research (Lipiński *et al.* 1998), and there have also been some theoretical advances in the same direction (e.g. Coelho *et al.*

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Manuscript received: October 1997

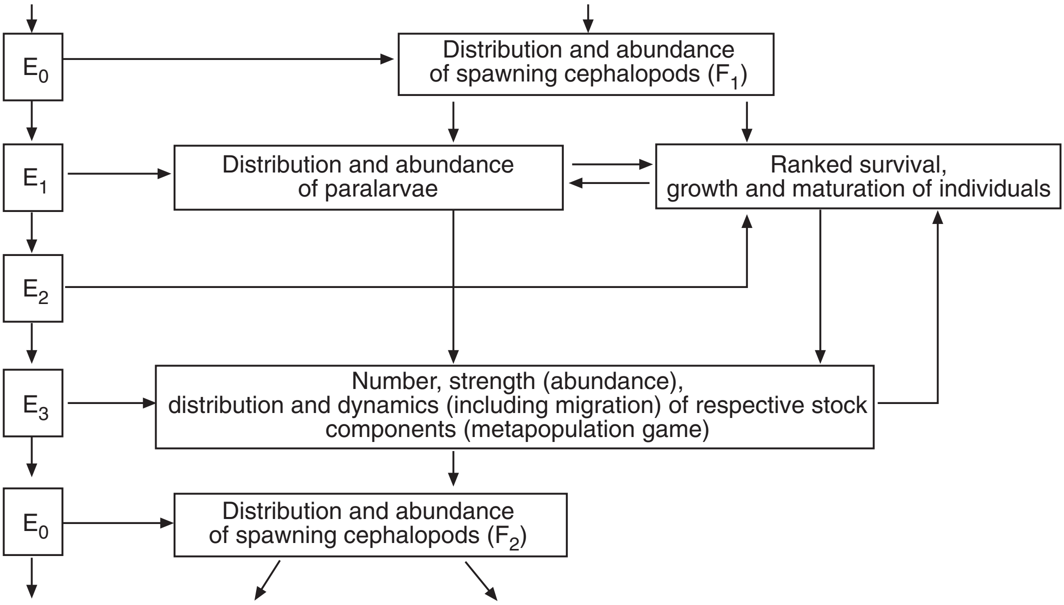


Fig. 1: Flow diagram of a cephalopod life cycle. E_0–E_3 represent environmental modifiers, which have an impact on the processes marked in the other consecutive blocks

1994). Intuitively, such holistic approaches seem to be appriopriate for poorly known species and families because they incorporate fishers' observations, which in turn determine the "behaviour" of the fishery. They also permit the assumptions of management models and/or procedures to be double-checked before their practical implementation. Finally, they allow for the development of a set of checks and balances in the management plan.

A holistic (life-cycle) approach to research and management may be described briefly as follows:

- the first phase involves the collection of basic life-cycle data on the exploited species,particularly with regard to the dynamics of its distribution and abundance;
- the second phase will develop predictive models of stock response to harvesting that incorporate information on the species' life history;
- the third phase involves developing fishery management procedures that incorporate the understanding gained in the first two phases.

Ideally, the three phases should be consecutive; in practice, they have to be explored almost simultaneously. Further, prediction-based scenarios should be flexible and operate within acceptable ranges of error and risk, instead of being confined to traditional, single units.

In this paper, a new concept in cephalopod resource management is discussed, one which emphasizes the importance of life-cycle research. It makes use of published data concerning cephalopod stocks worldwide, although the main evidence is drawn from the author's experience with *Illex* species (Lipiński 1981) and with *Loligo vulgaris reynaudii* (Augustyn *et al*. 1992, 1994, Lipiński 1992). Overall, the paper aims to generate ideas for further investigation and is therefore qualitative in nature. The level of generalization includes most commercially exploited species from the following families of cephalopods: Octopodidae, Sepiidae, Loliginidae, Ommastrephidae and Gonatidae. The fish taxa used are limited to marine, commercially exploited groundfish species (e.g. hake *Merluccius* spp.).

CHARACTERISTICS OF CEPHALOPOD LIFE CYCLES

General

The general understanding of the cephalopod life cycle required for management purposes is presented in Figure 1; it applies to populations consisting of single-year, non-overlapping generations. Therefore, the distribution and abundance of spawning cephalopods determines the distribution and abundance of paralarvae, whose individually ranked rates of mortality, growth and maturation in turn determine the stock composition (which itself influences mortality, growth and maturation). The adult stock, the spawners, takes part in the main metapopulation survival game (McQuinn 1997) of the species. Clearly, Figure 1 could not apply to most groundfish species, because the assumption of single-year, non-overlapping generations would be violated.

The role of environmental modifiers (kept to a minimum in Fig. 1) is beyond the scope of this paper. Their characteristics are the subject of other studies (Roberts and Sauer 1994, Roberts 1998). Environmental modifiers themselves constitute a whole set of important factors, rather than a single parameter (e.g. temperature). Cause-and-effect elements between these modifiers are integral to the temporal flow of environmental conditions (represented by arrows between blocks marked E in Fig. 1).

Whether diagrams/models such as that of Figure 1 are realistic from a research perspective is currently being tested for the South African chokka squid *Loligo vulgaris reynaudii*. Information on environmental variables and the distribution and abundance of spawning squid (Augustyn *et al.* 1992, 1994) can be collected and then linked using a model (Roberts 1998). Survival (Lipiński *et al.* in prep.), growth (Lipiński and Durholtz 1994), maturation (Lipiński and Underhill 1995) and a metapopulation structure and dynamics (Augustyn *et al.* 1992, 1994) have been described and modelled. In some other species, however, collection of all necessary data may be difficult (e.g. distribution and abundance of spawning *Illex illecebrosus*; Hatanaka *et al.* 1985), but then these data may be inferred from other sources (Coelho *et al.* 1994, O'Dor *et al.* 1997).

Life-cycle parameters

Fecundity in cephalopods is dependent on their size and mass which, in turn, are often temperature-related (Forsythe 1993, Roeleveld *et al.* 1993). Fecundity is clearly linked to the survival strategy of the species (Doi and Kawakami 1979, Lipiński *et al.* in prep.). Life cycles are generally short, individual variation large and metapopulation structure complicated, loose and variable (Boyle and Boletzky 1996). Discrete populations are typically difficult to identify, and a metapopulation concept may, therefore, be useful (McQuinn 1997). Cephalopods differ from fish in their lack of the *milieu interieur* (Lipiński 1992). In contrast, they exhibit great physiological plasticity (O'Dor and Shadwick 1989), which results in substantial individual variability in rates of growth and maturity. The life cycle may be characterized by long paralarval and juvenile phases, followed by a period of rapid, exponential growth, which slows or stops during breeding (Jackson 1994).

Strong migration patterns and temporal and spatial synchronization of maturation processes make mass spawning concentrations possible (Sauer *et al.* 1992). However, maturation processes are themselves complex and seem to be highly sensitive to short-term environmental stress (e.g. temperature, darkness, lack of food; M. J. Roberts, Sea Fisheries, pers. comm.). Sexual maturity may be attained in various geographical localities within a distributional range, not only on the main spawning grounds.

The intrinsic factors that regulate cephalopod paralarval survival are very important; it is suspected that starvation plays a much greater role as a mortality factor in cephalopod paralarvae than in fish larvae (Letcher *et al.* 1996, Lipiński *et al.* in prep.). Regrettably, the only data available for making such an inference are based on aquarium observations related to the mechanism of prey capture, rejection or acceptance, and learning processes associated with this (LaRoe 1971, Hurley 1976, Yang *et al.* 1986, Lee *et al.* 1994, Chen *et al.* 1996). While such observations and experiments can be usefully continued to include predation impact, the difficulties of differentiating and quantifying predation- and starvation-related mortality directly in the sea still remain.

SPATIAL DYNAMICS OF CEPHALOPOD POPULATIONS

Cephalopods and fish: the main ecological point of departure

The key to understanding the ecological success or failure of cephalopod species lies in interpretation of the roles of spatial and temporal scales in their life cycle. These are important, because they are reversed in cephalopod and fish life histories; therefore, they represent a major point of ecological departure between the two groups (O'Dor 1998).

In most marine fish, optimal ontogeny favours a short larval phase and a long adult life, with two or more spawning events (iteroparity). Their survival depends to a large extent on predator-prey relationships (Letcher *et al.* 1996).

In summary, in most exploited marine groundfish:

- the larval phase of their growth is relatively short and, consequently, they are transported passively for a short time only;

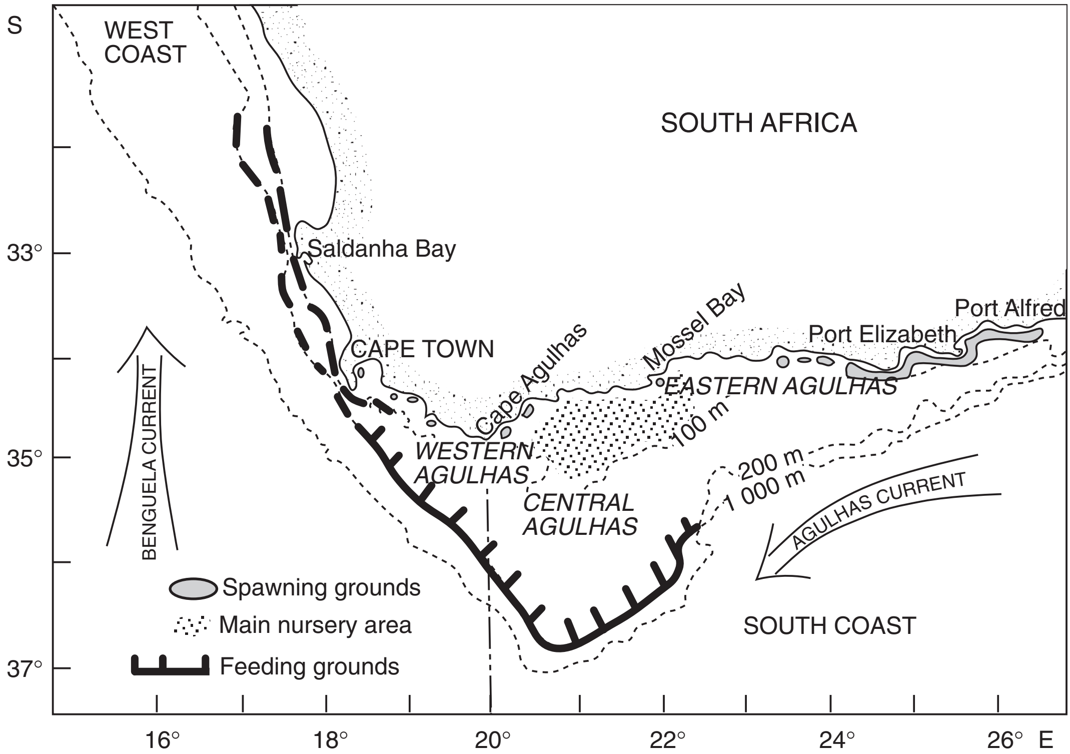


Fig. 2: Qualitative spatial scale of the life cycle of *Loligo vulgaris reynaudii*

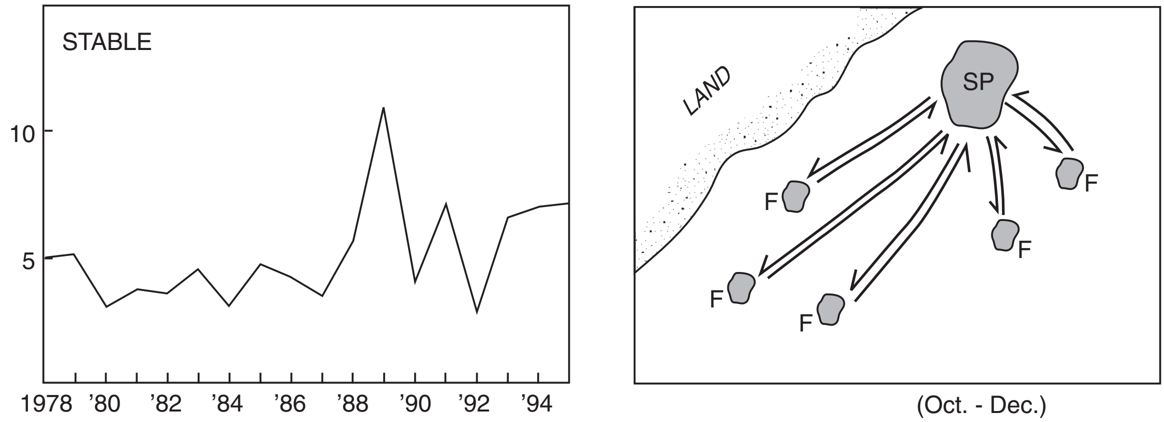
- their survival is at least equally or more predator-prey related than related to factors leading to starvation (interpretation based on the results of Letcher *et al*. 1996);
- habitat selection on the shelf presents relatively little constraint to either juveniles or adults – energetics, resources and time are available.

Owing to the overlapping generations in fish populations, they are well equipped to counter sudden, and drastic, reductions in their numbers. The life-cycle properties listed above have allowed large-scale, sustainable (or at least semi-sustainable; Pauly *et al*. 1998) fisheries for many groundfish species to develop.

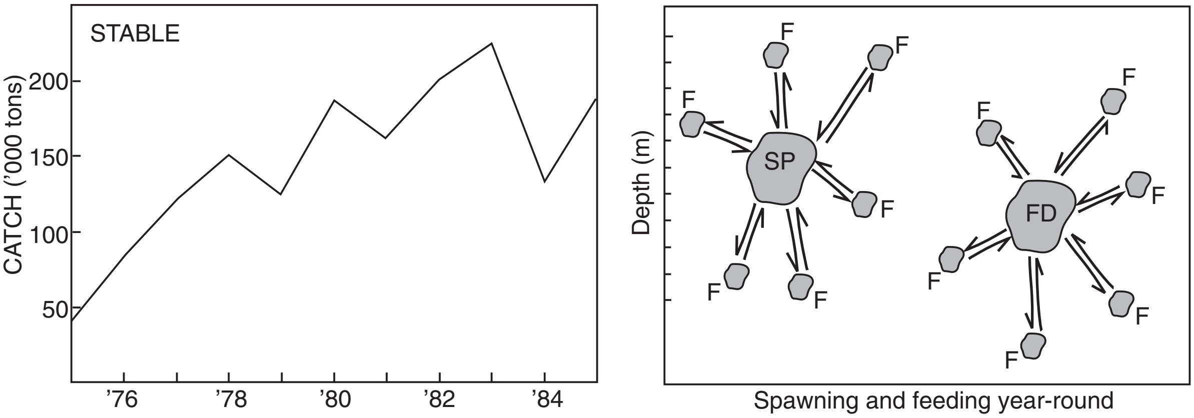
Cephalopod paralarvae are better equipped energetically than adults (i.e. their loss of energy in swimming, catching prey, etc. is relatively smaller than that of adults; O'Dor and Webber 1986, O'Dor *et al.* 1986). Survival of cephalopod paralarvae is largely dependent on their ability to avoid starvation and is therefore linked to a learning process (Lipiński *et al.* in prep.). In contrast to the paralarval period, cephalopod adults do not enjoy the energetic advantages which fish do (O'Dor and Webber 1986). Physiological and ecological commitments are stretched to their limits during this latter phase, which is characteristically short (O'Dor and Shadwick 1989, Boyle and Boletzky 1996).

In cephalopods such as *Loligo vulgaris reynaudii*, paralarvae, juveniles and adults of the same population separate and become spatially distinct. Such a distribution is determined by prevailing water movements (which are, of course, influenced by winds and currents) and the availability of appropriate food. The influence of predation pressure in this respect is poorly understood. In more general terms, the metapopulation survival game of *L. v. reynaudii* is played between the main spawning and feeding grounds. The game is won for the species if enough back-up spawners exist at any given time in any part of the range of the species to compensate for all possible large-scale disasters (including capture by fisheries) which may occur in another part of the range. This safety mechanism in *L. v. reynaudii* is spatial, and when the main aggregations form on the spawning grounds, it will operate mainly on the feeding grounds (Fig. 2). In addition, a small proportion

(a) *Loligo vulgaris reynaudii*



(b) *Ommastrephes bartramii*



(c) *Todarodes pacificus*

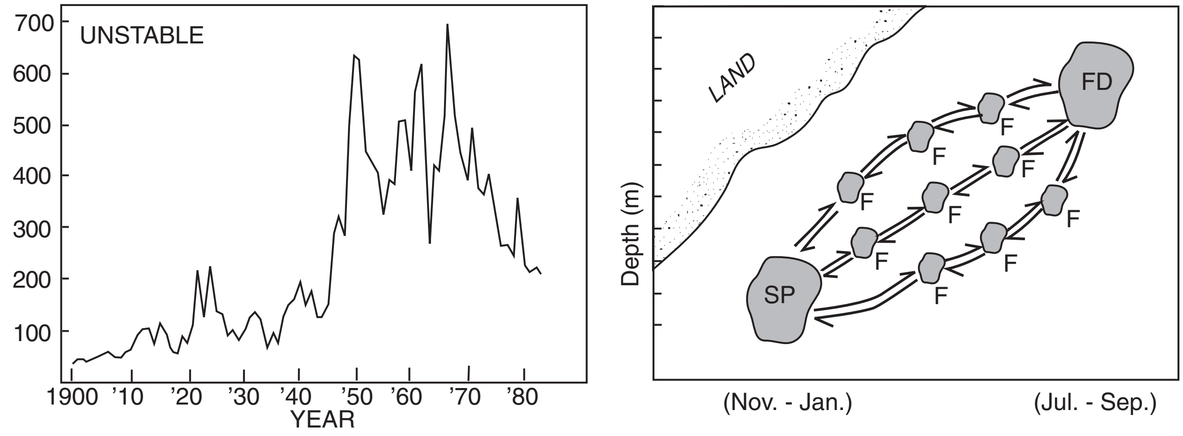


Fig. 3: Patterns of catches and of feeding and spawning of three species of squid – (a) *Loligo vulgaris reynaudii,* (b) *Ommastrephes bartramii,* (c) *Todarodes pacificus* (SP = spawning concentrations, FD = feeding aggregations, F = nonspecific small schools

of the metapopulation is on the move all the time and may also act as a buffer against sudden or prolonged disasters (Sauer *et al.* 1997, Lipiński *et al.* 1998). In some squid species, however, these safety mechanisms do not work well. Examples are the metapopulations of *Illex illecebrosus* (Coelho *et al.* 1994) and *Todarodes pacificus* around Japan (Murata 1989). In both cases, large feeding aggregations, which were the target of fisheries, collapsed as a result of drastic and sudden reductions in abundance from one year to the next.

It is suspected that the stability of stocks of and fisheries for cephalopods such as *Loligo vulgaris reynaudii* and *Ommastrephes bartramii* is dependent upon difficult-to-predict and multi-factored external variables acting on a complicated metapopulation structure (Lipiński 1996). In such a scenario, the metapopulation is fragmented into a multitude of small units (mostly hunting schools) which occupy the whole spatial range of the species. Each of these units acts like a single generation in fish, so enhancing the probability of survival of the species in the event of a sudden biomass reduction anywhere within the range. On the other hand, when the metapopulation is highly structured (e.g. the number of spatial units is small in a part of or in the whole species range, but the numbers of individuals in each unit are very large), the same factors result in unstable, unpredictable stocks and fisheries (e.g. *Illex illecebrosus* and *Todarodes pacificus*, Fig. 3). However, even within such metapopulations, the basic pattern of the life cycle and the spatial safeguards (see above) are sufficient to preserve the species and to pave the way for complete recovery (Sakurai *et al.* 1997). There are, of course, the intermediate cases (e.g. *Illex argentinus*), where the number of units is large, and where the numbers of individuals in many units are very large.

In *Loligo vulgaris reynaudii*, there may be some systematic patterns between years with regard to spatial and temporal shifts in abundance. For example, Roel (1998) detected two opposing trends in abundance indices for the metapopulation over time, on the same fishing grounds. The groundfish research survey results showed an increase, while both bycatches of *L. v. reynaudii* in the trawl fishery and catch rates in the directed jig fishery decreased. In the present author's opinion, the explanation may lie in a systematic and natural annual variation in the biomass within a given year, particularly during the period during which a survey is conducted. This increase may be linked to the beginning of an eastward migration of squid preceding the main spawning season (September survey) or to an offshore migration of squid to spawn in deeper water (April/May survey; Roberts and Sauer 1994). In both cases, such migrations could make squid more accessible to bottom gear on the trawlable grounds. Of course, there are other opinions (Roel 1998).

In summary, most commercially exploitable cephalopod populations exhibit the following characteristics:

- the paralarval and early juvenile period of growth is of relatively long duration, resulting in a protracted period of passive transport;
- paralarval survival is linked to an ability to stave off starvation, i.e. learning how to capture prey is very important;
- habitat selection has severe constraints, energetic costs are high, reserves are often lacking and generation times (longevities) are short;
- the adult phase is short.

As a consequence, spatial distribution is a very important limiting factor for cephalopod survival. The success or failure of each generation may be decided by the geographic and micro-habitat distribution of the preceding generation.

USE OF LIFE-HISTORY INFORMATION IN MANAGEMENT

Various implications for possible approaches to management can be drawn from the ideas outlined above. Two examples are described below.

The CIAC '97 Fisheries Workshop that dealt with cephalopod resource management concluded that the most important key feature of cephalopod fisheries biology was that "...most exploited squid species have a very short lifespan (annual or subannual), thus the only manner which catch levels in one year affect abundance in the next is through the stock-recruitment relationship" (Lipiński *et al.* 1998). Such a stock-recruitment relationship may be represented graphically (Fig. 4). Even if it is assumed that the spawning stock and paralarva abundance indices can be obtained easily, the size of the spawning stock will always be linked to immigration into the fished stock. Therefore, the spawning stock in the following year cannot be deduced only from the number of recruits at the onset of the fishing season (e.g. in spring for chokka *Loligo vulgaris reynaudii*). In such a case, the stock-recruitment relationship as well as the quantitative spatial strategy of the species have to be known to attempt to predict (i.e. assess the stock dynamics) the abundance of squid for the next year.

A second example, also from the *L. v. reynaudii* fishery, deals with calculations of the Sustainable Spawning Biomass (SSB), which are very useful in planning the management of resources, even if the proportional escapement strategy is not an option (Au-

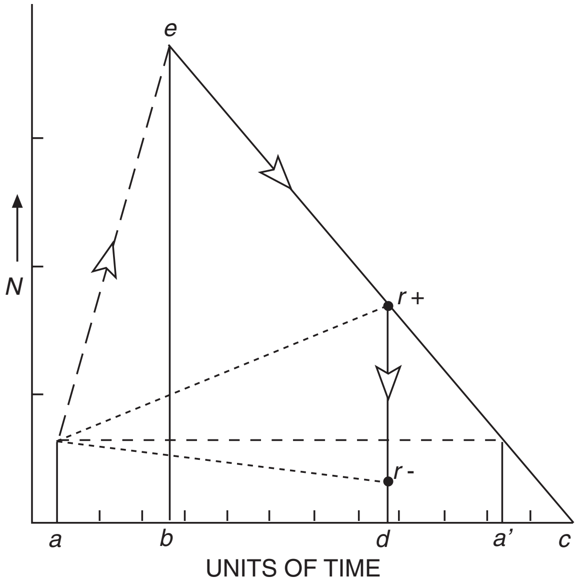


Fig. 4: Graphic representation of the stock-recruitment relationship in *Loligo vulgaris reynaudii*. *N* = numbers, *a* = spawning stock, *a'* = resultant spawning stock, *b* = hatchlings, *c* = end of life of the whole generation, *d* = recruits. At any time the number of surviving individuals (Line e – c) may suddenly drop (e.g. line between *r*+ and *d*)

gustyn *et al.* 1993). The spatial distribution of squid (Fig. 2), which impacts the species' strategy for survival, makes it difficult to do a straightforward SSB calculation. If this were done for the spawning grounds only (where most of the fishing takes place), it would miss the large reserve components (stock reserves) on the Agulhas Bank, away from the spawning grounds. However, SSB calculations for the latter area will obviously have to be very different from those applicable to the spawning grounds. To accommodate such differences in one management plan will obviously require a detailed, quantitative knowledge of the spatial survival strategy on a species level.

ACKNOWLEDGEMENTS

These ideas were influenced by the input of many colleagues during the CIAC '97 Workshops and Symposium. Changes reflecting this input were made to the draft manuscript at the revision stage and, *inter alia*, were suggested by by the reviewers. My colleagues Dr R. L. Tilney and the first editor of this volume helped the clarity of the manuscript by getting rid of the Polish in my English. Very useful comments on an early draft were also made by Dr S. des Clers (formerly Imperial College, London) and an anonymous reviewer.

LITERATURE CITED

AUGUSTYN, C. J., LIPIŃSKI, M. R. and W. H. H. SAUER 1992 — Can the *Loligo* squid fishery be managed effectively? A synthesis of research on *Loligo vulgaris reynaudii*. In *Benguela Trophic Functioning*. Payne, A. I. L., Brink, K. H., Mann, K. H. and R. Hilborn (Eds). *S. Afr. J. mar. Sci.* **12**: 903–918.

AUGUSTYN, C. J., LIPIŃSKI, 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.

AUGUSTYN, C. J., ROEL, B. A. and K. L. COCHRANE 1993 — Stock assessment in the chokka squid *Loligo vulgaris reynaudii* fishery off the coast of South Africa. In *Recent Advances in Cephalopod Fisheries Biology.* Okutani, T., O'Dor, R. K. and T. Kubodera (Eds). Tokyo; Tokai University Press: 3–14.

BEDDINGTON, J. R. 1997 — Issues and outcomes for Theme 5. What is the scope for development of wild stock fisheries? In *Developing and Sustaining World Fisheries Resources. The State of Science and Management. Proceedings of the Second World Fisheries Congress, Brisbane, July 1996.* Hancock, D. A., Smith, D. C., Grant, A. and J. P. Beumer (Eds). Collingwood, Australia; CSIRO Publishing: 625–627.

BOYLE, P. R. and S. von BOLETZKY 1996 — Cephalopod populations: definition and dynamics. *Phil. Trans. R. Soc. Lond.* **351B**: 985–1002.

CHEN, D. S., VAN DYKHUIZEN, G., HODGE, J. and W. F. GILLY 1996 — Ontogeny of copepod predation in juvenile squid (*Loligo opalescens*). *Biol. Bull. mar. biol. Lab., Woods Hole* **190**: 69–81.

CLARKE, M. R. 1996a — The role of cephalopods in the world's oceans: an introduction. *Phil. Trans. R. Soc. Lond.* **351B**: 979–983.

CLARKE, M. R. (Ed.) 1996b — *The Role of Cephalopods in the World's Oceans. Phil. Trans. R. Soc. Lond.* **351B**: 977–1112.

COELHO, M. L., STOBBERUP, K. A., O'DOR, R. [K.] and E. G. DAWE 1994 — Life history strategies of the squid, *Illex illecebrosus*, in the Northwest Atlantic. *Aquat. Living Resour.* **7**: 233–246.

DOI, T. and T. KAWAKAMI 1979 — Biomass of Japanese common squid *Todarodes pacificus* Steenstrup and the management of its fishery. *Bull. Tokai reg. Fish. Res. Lab.* **99**: 65–83 (in Japanese).

F.A.O. 1997 — Yearbook of fisheries statistics. Catches and landings, 1995. *F.A.O. Fish. Ser.* **80**: 716 pp.

FORSYTHE, J. W. 1993 — A working hypothesis of how seasonal temperature change may impact the field growth of young cephalopods. In *Recent Advances in Cephalopod Fisheries Biology.* Okutani, T., O'Dor, R. K. and T. Kubodera (Eds). Tokyo; Tokai University Press: 133–143.

GREENWOOD, P. H., ROSEN, D. E., WEITZMAN, S. H. and G. S. MYERS 1979 — Phyletic studies of teleostean fishes, with a provisional classification of living forms. In *Readings in Ichthyology.* Love, M. S. and G. M. Cailliet (Eds). Santa Monica, California; Goodyear Publishing: 73–94.

HATANAKA, H., KAWAHARA, S., UOZUMI, Y. and S. KASA-

HARA 1985 — Comparison of life cycles of five ommastrephid squids fished by Japan: *Todarodes pacificus, Illex illecebrosus, Illex argentinus, Nototodarus sloani sloani* and *Nototodarus sloani gouldi*. *NAFO scient. Coun. Stud.* **9**: 59–68.

HINEGARDNER, R. and D. E. ROSEN 1979 — Cellular DNA content and the evolution of teleostean fishes. In *Readings in Ichthyology.* Love, M. S. and G. M. Cailliet (Eds). Santa Monica, California; Goodyear Publishing: 112–136.

HURLEY, A. C. 1976 — Feeding behavior, food consumption, growth, and respiration of the squid *Loligo opalescens* raised in the laboratory. *Fishery Bull., Wash.* **74**(1): 176–182.

JACKSON, G. D. 1994 — Application and future potential of statolith increment analysis in squids and sepioids. *Can. J. Fish. aquat. Sci.* **51**: 2612–2625.

LANGTON, R. W., AUSTER, P. J. and D. C. SCHNEIDER 1995 — A spatial and temporal perspective on research and management of groundfish in the Northwest Atlantic. *Revs Fish. Sci.* **3**(3): 201–229.

LaROE, E. T. 1971 — The culture and maintenance of the loliginid squids *Sepioteuthis sepioidea* and *Doryteuthis plei*. *Mar. Biol.* **9**(1): 9–25.

LEE, P. G., TURK, P. E., YANG, W. T. and R. T. HANLON 1994 — Biological characteristics and biomedical applications of the squid *Sepioteuthis lessoniana* cultured through multiple generations. *Biol. Bull. mar. biol. Lab., Woods Hole* **186**: 328–341.

LETCHER, B. H., RICE, J. A., CROWDER, L. B. and K.A. ROSE 1996 — Variability in survival of larval fish: disentangling components with a generalized individual-based model. *Can. J. Fish. aquat. Sci.* **53**: 787–801.

LIPIŃSKI, M. [R.] (Ed.) 1977 — *Squid Symposium, Gdynia, June 5–6, 1973.* Warsaw; Foreign Scientific Publications: 120 pp.

LIPIŃSKI, M. [R.] 1981 — Systematyczne i ewolucyjne znaczenie zmiennosci kalmarów z rodzaju *Illex* [Systematic and evolutionary significance of variability in squids from the genus *Illex*]. Ph.D. thesis, Uniwersytet Gdanski: 196 pp.

LIPIŃSKI, M. R. 1992 — Cephalopods and the Benguela ecosystem: trophic relationships and impact. In *Benguela Trophic Functioning.* Payne, A. I. L., Brink, K. H., Mann, K. H. and R. Hilborn (Eds). *S. Afr. J. mar. Sci.* **12**: 791–802.

LIPIŃSKI, M. R. 1996 — Squid fisheries of the world: chaos or pattern? In *Second World Fisheries Congress, Brisbane, July 1996, Proceedings* **1.** Hancock, D. A. and J. P. Beumer (Eds). Brisbane, Australian Society for Fish Biology: 22–23 (Abstract only).

LIPIŃSKI, M. R., BUTTERWORTH, D. S., AUGUSTYN, C. J., BRODZIAK, J. F. K., DES CLERS, S., O'DOR, R. K., PAULY, D., PURCHASE, L.V., ROBERTS, M. J., ROEL, B. A., SAKURAI, Y. and W. H. H. SAUER 1998 — Cephalopod fisheries: a future global upside to past over-exploitation of living marine resources? Results of an international workshop, 31 August - 2 September 1997, Cape Town, South Africa. 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**: 463–469.

LIPIŃSKI, M. R. and M. D. DURHOLTZ 1994 — Problems associated with ageing squid from their statoliths: towards a more structured approach. *Antarctic Sci.* **6**(2): 215–222.

LIPIŃSKI, M. R., HAMPTON, I., SAUER, W. H. H. and C. J. AUGUSTYN 1998 — Daily net emigration from a spawning concentration of a chokka squid (*Loligo vulgaris reynaudii* d'Orbigny, 1845) in Kromme Bay, South Africa. *ICES J. mar. Sci.* **55**: 260–272.

LIPIŃSKI, M. R. and L. G. UNDERHILL 1995 — Sexual maturation in squid: quantum or continuum? *S. Afr. J. mar. Sci.* **15**: 207–223.

LIPIŃSKI, M. R., WISSEL, C. and R. NAVARRO (in preparation) — A model of loliginid squid survival (Cephalopoda: Loliginidae).

MANGEL, M., TALBOT, L. M., MEFFE, G. K., AGARDY, T., ALVERSON, D. L., BARLOW, J., BOTKIN, D. B., BUDOWSKI, G., CLARK, T., COOKE, J., CROZIER, R. H., DAYTON, P. K., ELDER, D. L., FOWLER, C. W., FUNTOWICZ, S., GISKE, J., HOFMAN, R. J., HOLT, S. J., KELLERT, S. R., KIMBALL, L. A., LUDWIG, D., MAGNUSSON, K., MALAYANG, B. S., MANN, C., NORSE, E. A., NORTHRIDGE, S. P., PERRIN, W. F., PERRINGS, C., PETERMAN, R. M., RABB, G. B., REGIER, H. A., REYNOLDS, J. E., SHERMAN, K., SISSENWINE, M. P., SMITH, T. D., STARFIELD, A., TAYLOR, R. J., TILLMAN, M. F., TOFT, C., TWISS, J. R., WILEN, J. and T. P. YOUNG 1996 — Principles for the conservation of wild living resources. *Ecol. Applications* **6**(2): 338–362.

McQUINN, I. H. 1997 — Metapopulations and the Atlantic herring. *Revs Fish Biol. Fish.* **7**: 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.

NESIS, K. N. 1987 — *Cephalopods of the World.* Neptune City, New Jersey; T.F.H. Publications: 351 pp.

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.

O'DOR, R. K., FOY, E. A., HELM, P. L. and N. BALCH 1986 — The locomotion and energetics of hatchling squid, *Illex illecebrosus*. *Am. malacol. Bull.* **4**(1): 55–60.

O'DOR, R. K., RODHOUSE, P. G. and E. G. DAWE 1997 — Squid recruitment in the genus *Illex*. In *Developing and Sustaining World Fisheries Resources. The State of Science and Management. Proceedings of the Second World Fisheries Congress, Brisbane, July 1996.* Hancock, D. A., Smith, D. C., Grant, A. and J. P. Beumer (Eds). Collingwood, Australia; CSIRO Publishing: 116–121.

O'DOR, R. K. and R. E. SHADWICK 1989 — Squid, the Olympian cephalopods. *J. Cephalopod Biol.* **1**(1): 33–55.

O'DOR, R. K. and D. M. WEBBER 1986 — The constraints on cephalopods: why squid aren't fish. *Can. J. Zool.* **64**: 1591–1605.

PAULY, D., CHRISTENSEN, V., DALSGAARD, J., FROESE, R. and F. TORRES 1998 — Fishing down marine food webs. *Science* **279**: 860–863.

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.

ROBERTS, M. J. and W. H. H. SAUER 1994 — Environment: the key to understanding the South African chokka squid (*Loligo vulgaris reynaudii*) life cycle and fishery? *Antarctic Sci.* **6**(2): 249–258.

ROEL, B. A. 1998 — Stock assessment of chokka squid *Loligo vulgaris reynaudii*. Ph.D. thesis, University of Cape Town. xi + 217 pp.

ROELEVELD, M. A. C., LIPIŃSKI, M. R. and M. G. VAN DER MERWE 1993 — Biological and ecological aspects of the distribution of *Sepia australis* (Cephalopoda: Sepiidae) off the south coast of southern Africa. *S. Afr. J. Zool.* **28**(2):

99–106.

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*. Cape Town; CIAC: 80–81.

SAUER, W. H. H., ROBERTS, M. J., LIPIŃSKI, M. R., SMALE, M. J., HANLON, R. T., WEBBER, D. M. and R. K. O'DOR 1997 — Choreography of the squid's "nuptial dance". *Biol. Bull. mar. Biol. Lab., Woods Hole* **192**(2): 203–207.

SAUER, W. H. H., SMALE, M. J. and M. R. LIPIŃSKI 1992 — The location of spawning grounds, spawning and schooling behaviour of the squid *Loligo vulgaris reynaudii* (Cephalopoda: Myopsida) off the Eastern Cape coast, South Africa. *Mar. Biol.* **114**: 97–107.

TEICHERT, C. 1988 — Main features of cephalopod evolution. In *The Mollusca.* **12.** *Paleontology and Neontology of Cephalopods.* Clarke, M. R. and E. R. Trueman (Eds). San Diego; Academic Press: 11–79.

TOMIYAMA, T. and T. HIBIYA (Eds) 1978 — *Fisheries in Japan. Squid and Cuttlefish*. Tokyo; Japan Marine Products Photo Materials Association: 161 pp.

YANG, W. T., HIXON, R. F., TURK, P. E., KREJCI, M. E., HULET, W. H. and R. T. HANLON 1986 — Growth, behavior, and sexual maturation of the market squid, *Loligo opalescens*, cultured through the life cycle. *Fishery Bull., Wash.* **84**(4): 771–798.