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## TIME, SPACE AND THE ECOPHYSIOLOGY OF SQUID GROWTH, LIFE IN THE FAST LANE

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SQUID GROWTH  
STATOLITHS  
AGE VALIDATION  
METABOLISM  
TELEMÉTRY

**ABSTRACT.** – Squids are important components of many marine ecosystems and continue to come under increasing commercial fishing pressure. In some heavily fished regions, squid have replaced their teleost competitors. They achieve this through rapid growth and short life spans. Valuable insights have been made regarding squid life histories by both statolith ageing studies and culture experiments where growth could be observed in the laboratory. These studies continue to reveal that most species of squid live for a year or less and there is only evidence from a small number of species for life spans longer than a year. Small warm water species can complete their life spans in just a few months. While there has been some recently published statolith increment validation experiments, there is a need for increased work in this area. Squids appear to have fast growth rates and short life spans due to: (1) a combination of efficient digestion with a protein based metabolism; (2) the ability to sustain continued growth by a combination of both an increase in muscle fibre size (hypertrophy) along with continual recruitment of new muscle fibres (hyperplasia); (3) efficient use of oxygen and (4) low levels of antioxidative defense. Heavy fishing pressure on large late maturing fishes may have irreversibly tipped the balance of the ecosystem in favour of the fast growing short-lived squids. Detailed studies of marine protected areas (MPA's) including the use of telemetry technology will help clarify if and how overfished ecosystems can be brought back to their original 'balance'.

CROISSANCE DU CALMAR  
STATOLITHES  
DATATION  
MÉTABOLISME  
TÉLÉMÉTRIE

**RÉSUMÉ.** – Les Calmars représentent une partie importante de nombreux écosystèmes marins et sont soumis à des pressions croissantes de la pêche commerciale. Dans certaines régions où la pêche est intensive, les Calmars ont remplacé leurs compétiteurs, les Poissons Téléostéens. Cette réussite est due à une croissance rapide et à un cycle de vie court. L'étude de la croissance du Calmar en laboratoire et de la datation par les statolithes a permis d'approfondir les connaissances sur son cycle de vie. La durée de vie de la plupart des espèces est de un an ou moins et quelques espèces seulement ont un cycle de vie supérieur à un an. Certaines espèces tropicales de petite taille complètent leur cycle de vie en quelques mois seulement. Des expériences de validation sur la croissance évaluée à partir des statolithes ont été publiées récemment. Cependant, il est nécessaire d'étendre les connaissances dans ce domaine. Les Calmars semblent avoir une croissance rapide et un cycle de vie court pour plusieurs raisons : (1) ils combinent une digestion efficace et un métabolisme protéinique ; (2) ils sont capables de maintenir une croissance continue en combinant un accroissement de la taille des fibres musculaires (hypertrophie) avec l'addition continue de nouvelles fibres (hyperplasie) ; (3) ils utilisent l'oxygène de manière efficace et (4) leur niveau de défenses antioxydantes est bas. La pêche intensive des espèces de Poisson à maturité tardive pourrait avoir modifié de manière irréversible l'équilibre de l'écosystème en faveur d'espèces à croissance rapide et à cycle de vie court. Des études détaillées utilisant notamment les techniques de télémétrie dans les zones marines protégées (ZMP) permettront de vérifier si les écosystèmes surexploités peuvent être ramenés à leur équilibre initial.

Considerable progress has been made in the last decade on the growth dynamics of squid. Studies continue to reveal elements of their life history that point to life spans that are short, growth rates that are rapid and populations that turnover quickly. Our best understanding of the dynamics of squid growth has arisen as a result of both controlled culture experiments (e.g., Lee *et al.* 1994, Forsythe *et al.* 2001) and statolith based ageing studies (e.g., Jackson *et al.* 1997). As a result we have better data on how squid grow and how this can impact the environment where they live.

Evidence now suggests that as longer lived finfish stocks have been depleted, they have been replaced by cephalopods (Pauly & Christensen 1995, Caddy & Rodhouse 1998). Circumstantial evidence strongly suggests that increased cephalopod abundance in Tunisian waters, the Adriatic Sea and the Gulf of Thailand is due to a decrease in the standing stock of groundfish competitors by half or more along with a decrease in predators (Caddy & Rodhouse 1998). Furthermore, it is likely that oceanic squid stocks may have increased due to a reduction in predators. In consideration of tuna consumption alone, Caddy & Rodhouse (1998) pointed out how tuna landings have risen from 2 to 4 million t  $y^{-1}$ . Given that tuna diet is approximately 25% oceanic squids and consumption is about 10% body weight  $d^{-1}$ , this 2 ton difference accounts for an extra 20 million t of squid in the world's oceans in recent years.

The reduction in traditional groundfish landings has resulted in squid stocks coming under increasing fishing pressure. While total world catch of groundfish has remained stable or decreased in recent years the catch of cephalopods has increased dramatically (Caddy & Rodhouse 1998). The growth dynamics of squid populations appear to be well suited to filling niches once their teleost competitors have been removed. They are essentially 'weeds of the sea' O'Dor (1998), filling spaces just as fast growing weeds quickly colonise an area of ground after a forest is felled. Rapid population turnover also provides challenges to those needing to sustainably manage squid fisheries (Murphy & Rodhouse 1999).

So where do we stand now with regard to our understanding of the population dynamics of squids? A comprehensive review of squid growth based on statolith ageing was compiled by Jackson (1994) and statolith-based loliginid studies were reviewed by Jackson (1998). The Jackson (1994) review summarised what ageing work had been carried out and how this data was used to model growth. To some extent, many of the studies covered in that review were simply a preliminary application of statolith increment counts. Since then work has expanded on both the mechanisms and dynamics of squid growth. This paper intends to

provide a status report of where we are in our understanding of squid growth.

### *Statolith validation*

An important area of research has been continuing work on statolith validation (e.g., Estácio *et al.* 1999) to verify the periodicity of statolith increments. Jackson (1994) reported validation studies for 11 squid species and one sepioid (*Idiosepius pygmaeus*). Since 1994 work has continued with validation studies (Table I). Especially noteworthy is the study of Lipinski *et al.* (1998a) as this study is the only one thus far to document directly, daily periodicity of adult squid in the wild. The number of studies is small which indicates the problems associated with maintaining squid successfully under experimental conditions. The results continue to support daily increment periodicity in statoliths and reveal the need for further work to be carried out with more species of squid and especially with oceanic and deep sea oegopsid squids.

The study by Arkhipkin *et al.* (1996) on *Berryteuthis magister* reveals that other indirect methods of age verification such as following modes may work for cold water species with discrete cohorts. However, trying to identify modes for many species in relation to age is not possible due to the extreme plasticity in squid growth and the poor relationship between size and age (Jackson *et al.* 2000a). Research by Villanueva (2000a) showed that increment periodicity was daily in *Loligo vulgaris* regardless of the culture temperature. However, this was not the case for *L. vulgaris* embryos (Villanueva 2000b). Work by Yatsu & Mori (2000) who compared known age paralarvae raised in culture to aged field-captured specimens indicated agreement in the form of growth for both groups which suggested that the statolith based field estimates were realistic descriptors of growth in paralarvae and young juveniles.

### *Statoliths as ageing tools*

A number of papers continue to use statoliths for routine ageing. The precision of statolith increment counts continues to be refined (Arkhipkin *et al.* 1998a, Durholtz & Lipinski 2000, Gonzalez *et al.* 1998, 2000, Jackson & Moltschanivskyj 1999) and the technique is becoming more widespread and incorporated into large scale studies (e.g., Arkhipkin 2000, Arkhipkin *et al.* 1998b, Bower 1996, Macy & Brodziak 2001). Since the review of Jackson (1994) there have been a number of studies that have undertaken a comprehensive ageing analysis for a variety of squid species (Table II)

An update of statolith based loliginid life history studies (Jackson 1998) included 17 species from

Table I. – Studies published since Jackson (1994) that have used validation techniques for statolith increment periodicity in squids.

| Species                          | Number of individuals | Technique  | Reference                       |
|----------------------------------|-----------------------|--|---------------------------------|
| <i>Loligo vulgaris reynaudii</i> | 8                     | Tetracycline staining in field                               | Lipinski et al. 1998a           |
| <i>Loligo vulgaris</i>           | 31                    | Tetracycline staining in culture                             | Villanueva 2000a                |
| <i>Loligo vulgaris</i> embryos   | 36                    | Tetracycline staining in culture                             | Villanueva 2000b                |
| <i>Loliolus noctiluca</i>        | 6                     | Tetracycline staining in culture                             | Dimmlich & Hoedt 1998           |
| <i>Lolliguncula brevis</i>       | 43                    | Tetracycline staining in culture                             | Jackson et al. 1997             |
| <i>Sepioteuthis lessoniana</i>   | 5                     | Alizarin red staining in culture                             | Balgos & Pauly 1998             |
| <i>Sepioteuthis lessoniana</i>   | 11                    | Tetracycline staining in culture                             | Jackson & Moltschaniwskyj 2001a |
| <i>Gonatus onyx</i>              | 4                     | Counting increments from capture stress check                | Arhipkin & Bizikov 1997         |
| <i>Gonatus borealis</i>          | 2                     | Counting increments from capture stress check                | Arhipkin & Bizikov 1997         |
| <i>Gonatus magister</i>          | 1                     | Counting increments from capture stress check                | Arhipkin & Bizikov 1997         |
| <i>Galiteuthis phyllura</i>      | 1                     | Observing increment from check                               | Arhipkin 1996a                  |
| <i>Eogonatus tinro</i>           | 4                     | Counting increments from capture stress check                | Arhipkin & Bizikov 1997         |
| <i>Berryteuthis magister</i>     | 88                    | Comparing statolith increments to gladius increments         | Arhipkin et al. 1996            |
| <i>Berryteuthis magister</i>     | 60                    | Comparing increment number to elapsed days between 2 cohorts | Arhipkin et al. 1996            |

around the world. Ages ranged from less than a hundred days for small warm water and tropical species (*Lolliguncula brevis* Jackson *et al.* 1997; *Loligo duvauceli* Chotiyaputta 1997) to around a year for more temperate species. However, of the 17 loliginids reviewed in Jackson (1998) only three had life spans of over a year (*Loligo vulgaris* Arhipkin 1995, *Heterololigo bleakeri* Kinoshita 1989, & *Loligo vulgaris reynaudii* Lipinski 1991). More recent work (Table II) also supports a life span > 1 yr for *L. vulgaris* (Raya *et al.* 1999) and possibly for *L. forbesi* as well (Rocha & Guerra 1999). The majority of loliginids however, appear to have life spans of less than a year.

Oegopsid squids also appear to not have extensive life spans (Table II). Only 7 species from recent studies have reported life spans of < 1 yr (*Berryteuthis magister*, *Nototodarus sloanii*, *N. gouldi*, *Martialia hyadesi*, *Gonatus fabrici*, *Ancistrocheirus lesueurii*, and *Architeuthis*) and only *Gonatus fabricii* has a life span of > 22 months. More surprising are the extremely short life spans of small tropical species such as *Pterygioteuthis gemmata* with a life span of < 3 months and *Abralia trigonura*, *Abraliopsis pfefferi* and *Loliolus noctiluca* with life spans < 6 months (Table II). Small tropical species appear to have an extremely rapid population turnover.

The majority of squid ages reviewed in Table II are based on assumed daily periodicity of statolith increments, as many have not been validated (Table I, see also Jackson 1994). However, advances in culture techniques provide a means to directly observe squid growth and life spans. There is now a substantial body of information available for a single squid species: the Indo-Pacific squid *Sepioteuthis lessoniana* which allows for a direct comparison of growth between culture experiments and field-based statolith ageing studies.

Statolith ageing and validation studies of *S. lessoniana* include Jackson (1990), Jackson & Choat (1992), Jackson *et al.* (1993), Jackson & Moltschaniwskyj (2001a) and, Balgos & Pauly (1998). Furthermore, a comprehensive seasonal/geographical ageing study of *S. lessoniana* was carried out by Jackson & Moltschaniwskyj (2001b) and reproductive strategies of *Sepioteuthis* were examined by Pecl 2001. In all these studies the post-hatching life cycle of *S. lessoniana* was less than 250 d. Moreover, there have been extensive culture experiments with this species both in Japan (Tsuchiya 1982, Segawa 1987), Texas USA (Lee *et al.* 1994, Forsythe *et al.* 2001) and in Thailand (Nabhitabhata 1995, 1996). All the culture studies indicate a life history of < 1 yr with growth to as much as 2 kg. The growth information for this species based on validated statolith age estimates and direct observation of growth of cultured individu-

Table II. – Studies published since Jackson (1994) that have used statolith increment counts to determine age and life spans of squids. See also Jackson (1998) for other studies of loliginid age and growth. The asterisk indicates pen length rather than mantle length.

| Species                          | Estimated maximum age (days)  | Mantle length (mm)              | Location                            | Comments   | Reference                       |
|----------------------------------|-------------------------------|---------------------------------|-------------------------------------|--|---------------------------------|
| <i>Loligo vulgaris</i>           | 361 (F)<br>382 (M)            | 255 (F)<br>383 (M)              | North-west Spain                    | Some seasonal variation in growth  | Rocha & Guerra 1999             |
| <i>Loligo vulgaris</i>           | 294 (F)<br>308 (M)            | 285 (F)<br>534 (M)              | Saharan Bank                        | Tropical   | Raya et al. 1999                |
| <i>Loligo vulgaris</i>           | 335 (F)<br>396 (M)            | 290 (F)<br>498 (M)              | Saharan Shelf                       | Tropical   | Arkhipkin 1995                  |
| <i>Loligo vulgaris</i>           | ~253 (F)<br>~288 (M)          | ~308 (F)<br>~311 (M)            | Southern Portugal                   | Warmwater  | Bettencourt et al. 1996         |
| <i>Loligo gahi</i>               | 366 (F)<br>339 (M)            | ~146 (F)<br>~169 (M)            | Patagonian Shelf                    | Seasonal variation in growth   | Hatfield 2000                   |
| <i>Loligo opalescens</i>         | 238(F)<br>243(M)              | ~128(F)<br>~138(M)              | California                          | No differences between males or females                                  | Butler et al. 1999              |
| <i>Loligo pealei</i>             | ~275 (F)<br>~295 (M)          | ~213 (F)<br>~295 (M)            | North-west Atlantic                 | Growth variable depending on season                                      | Brodziak & Macy 1996            |
| <i>Lolliguncula brevis</i>       | 172 (F)<br>150 (M)            | 72 (F)<br>61 (M)                | Gulf of Mexico                      | Growth variable depending on season                                      | Jackson et al. 1997             |
| <i>Sepioteuthis lessoniana</i>   | 173 (F)<br>224 (M)            | 276 (F)<br>256 (M)              | Australia, Thailand                 | Subtropical, tropical, seasonal/geographical differences in growth rates | Jackson & Moltschaniwskyj 2001b |
| <i>Sepioteuthis lessoniana</i>   | ~186 (F)<br>~174(M)           | ~174 (F)<br>~212 (M)            | Australia                           | Tropical   | Semmens & Moltschaniwskyj 2000  |
| <i>Photololigo</i> sp.           | ~91                           | ~102                            | Northeastern Australia              | Tropical   | Moltschaniwskyj 1995            |
| <i>Photololigo</i> sp. 1         | 158 (F)<br>119 (M)            | 115 (F)<br>87 (M)               | Northwest Shelf of Australia        | Tropical   | Jackson & Yeatman 1996          |
| <i>Loliolus noctiluca</i>        | ~250 (F)<br>~256 (M)          | ~69 (F)<br>~54 (M)              | Eastern Australia ~38°S             | Temperate  | Dimmlich & Hoedt 1998           |
| <i>Loliolus noctiluca</i>        | 148 (F)<br>129 (M)            | 80 (F)<br>52 (M)                | Eastern Australia ~33°S             | Temperate  | Jackson & Moltschaniwskyj 2001c |
| <i>Loliolus noctiluca</i>        | 121 (F)<br>107 (M)            | 54 (F)<br>61 (M)                | Eastern Australia ~19°S             | Tropical, seasonal variation in growth                                   | Jackson & Moltschaniwskyj 2001c |
| <i>Loligo forbesi</i>            | 514 (F)<br>480 (M)            | 322 (F)<br>400 (M)              | North-west Spain                    | Some seasonal variation in growth  | Rocha & Guerra 1999             |
| <i>Abralia trigonura</i>         | 188 (F)<br>182 (M)            | ~36 (F)<br>~31 (M)              | Hawaii                              | Abundant species in mesopelagic boundary community                       | Young & Mangold 1994            |
| <i>Abraliopsis pfefferi</i>      | 154 (F)<br>127 (M)            | 33 (F)<br>25 (M)                | Central East Atlantic               | Tropical, small, short life span   | Arkhipkin 1996c                 |
| <i>Ancistrocheirus lesueurii</i> | 609 (F)<br>360 (M)            | 423 (F)<br>90 (M)               | Central-East Atlantic               | Females strikingly larger and older than males                           | Arkhipkin 1997b                 |
| <i>Pterygoteuthis gemmata</i>    | 77 (F)<br>~73 (M)             | 30 (F)<br>~26 (M)               | Central East Atlantic               | Tropical, extremely short life span < 3 months                           | Arkhipkin 1997a                 |
| <i>Onychoteuthis banksi</i>      | 261 (F)<br>224 (M)            | 130 (F)<br>77 (M)               | Atlantic, Pacific and Indian Oceans | Females not mature, full life span not known                             | Arkhipkin & Nigmatullin 1997    |
| <i>Moroteuthis ingens</i>        | 358 (F)<br>393 (M)            | 544 (F)<br>382 (M)              | New Zealand                         | Sexually dimorphic with females bigger                                   | Jackson 1997                    |
| <i>Gonatus fabricii</i>          | ~644 (F)<br>654 (M)           | ~205* (F)<br>182* (M)           | Norwegian Sea                       | Arctic, suggested 2 year life cycle                                      | Arkhipkin & Bjørke 2000         |
| <i>Berryteuthis magister</i>     | 473 (M)<br>479 (F)            | 295 (M)<br>369 (F)              | Bering Sea                          | Coldwater  | Arkhipkin et al. 1996           |
| <i>Architeuthis</i>              | 294 (M)<br>375 (M)<br>422 (M) | 1028 (M)<br>975 (M)<br>1084 (M) | Off Ireland                         | All mature males   | Lordan et al. 1998              |
| <i>Illex illecebrosus</i>        | ~247 (F)<br>~216 (M)          | ~280 (F)<br>~246 (M)            | Newfoundland                        | Growth variable depending on season of hatch                             | Dawe & Beck 1997                |
| <i>Illex illecebrosus</i>        | ~198                          | ~205                            | Nova Scotian shelf                  |  | Arkhipkin & Fetisov 2000        |
| <i>Illex coindetii</i>           | 286 (F)<br>233 (M)            | 300 (F)<br>203 (M)              | Western Sahara                      | 2 groups (young 0.5 yr and older ~1yr maturing squid)                    | Arkhipkin 1996b                 |
| <i>Illex coindetii</i>           | 242 (F)<br>189 (M)            | 190 (F)<br>140 (M)              | Sierra Leone                        | Tropical   | Arkhipkin 1996b                 |

Table II. – (continued).

|                                  |                      |                      |  |   |  |
|----------------------------------|----------------------|----------------------|--|---|--|
| <i>Illex coindetii</i>           | 176 (F)<br>191 (M)   | ~159 (F)<br>~124 (M) | Central Mediterranean                        | Warmwater   | Arkhipkin et al. 1999a                 |
| <i>Illex coindetii</i>           | 240 (F)<br>230 (M)   | 197 (F)<br>143 (M)   | Central Mediterranean                        | Warmwater   | Arkhipkin et al. 2000                  |
| <i>Illex coindetii</i>           | ~422 (M)<br>477 (F)  | ~164 (M)<br>~201 (F) | Spanish Mediterranean                        | Warmwater, summer population appeared to grow faster than winter population | Sánchez 1995                           |
| <i>Illex coindetii</i>           | ~442 (F)<br>~380 (M) | ~377 (F)<br>~243 (M) | NW Spain                                     | Seasonal variation in growth  | González et al. 1996                   |
| <i>Todarodes sagittatus</i>      | 409 (F)              | 473 (F)              | Irish & Scottish waters                      | Larger squid were deeper suggesting ontogenetic downward migration          | Lordan et al. 2001                     |
| <i>Todarodes sagittatus</i>      | 262 (F)<br>231 (M)   | 319 (F)<br>201 (M)   | Western Sahara                               | Tropical  | Arkhipkin et al. 1999b                 |
| <i>Todaropsis eblanae</i>        | 220 (F)              | 139 (F)              | North West African Shelf                     | Tropical, suggested 1 year life span  | Arkhipkin & Laptikhovsky 2000          |
| <i>Nototodarus sloanii</i>       | 374 (F)              | 406 (F)              | New Zealand                                  | Seasonal variation in growth  | Uozumi 1998                            |
| <i>Nototodarus gouldi</i>        | 373                  | 376                  | New Zealand                                  | Seasonal variation in growth  | Uozumi 1998                            |
| <i>Nototodarus hawaiiensis</i>   | 195 (F)<br>192 (M)   | 183 (F)<br>164 (M)   | North West Slope of Australia                | Tropical  | Jackson & Wadley 1998                  |
| <i>Martialia hyadesi</i>         | 357 (F)<br>330 (M)   | ~343 (F)             | Patagonian Shelf                             | Cool, no mature females   | González et al. 1997                   |
| <i>Martialia hyadesi</i>         | 399 (F)<br>354 (M)   | 398 (F)<br>295 (M)   | South-west Atlantic                          | Coldwater   | Arkhipkin & Silvanovich 1997           |
| <i>Martialia hyadesi</i>         | 330 (F)<br>360 (M)   | 330 (F)<br>314 (M)   | South Georgia                                | Coldwater   | González & Rodhouse 1998               |
| <i>Ommastrephes bartramii</i>    | 306 (F)              | 454 (F)              | North Pacific                                | Small sample size   | Yatsu et al. 1998                      |
| <i>Ommastrephes bartramii</i>    | ~306 (F)<br>~306 (M) | ~458 (F)<br>~348 (M) | North Pacific                                | Some seasonal and geographical differences in growth rates                  | Yatsu et al. 1997, see also Yatsu 2000 |
| <i>Ornithoteuthis antillarum</i> | 182 (F)<br>173 (M)   | 117 (F)<br>83 (M)    | Central-east Atlantic                        | tropical  | Arkhipkin et al. 1998c                 |
| <i>Thysanoteuthis rhombus</i>    | 305 (F)<br>309 (M)   | 750 (F)<br>770 (M)   | Eastern tropical Atlantic/ Southwest Pacific | One of fastest growing squid species  | Nigmatullin et al. 1995                |
| <i>Cranchia scabra</i>           | 166 (F)              | 118 (F)              | Central East Atlantic                        | Tropical, fast growing, life span unknown only immature individuals         | Arkhipkin 1996d                        |
| <i>Liocranchia reinhardti</i>    | 146 (M)              | 183 (M)              | Central East Atlantic                        | Tropical, fast growing, life span unknown only immature individuals         | Arkhipkin 1996d                        |

als throughout their life cycle is unambiguous (see also Jackson *et al.* 2000a). We thus have a high degree of confidence in the growth rate and life span data for this loliginid. The synopsis of the research over the last several years along with earlier reviews (Rodhouse & Hatfield 1990, Jackson 1994, 1998) suggests that in fact it is difficult to find many squid species older than a year. Furthermore, extensive studies have revealed that growth of squid is very plastic and growth rates vary according to changes in temperature (Forsythe 1993, Forsythe *et al.* 2001, Hatfield 2000, Jackson & Moltschaniwskyj, 2001b, 2001c).

### Mechanisms responsible for squid growth

Squids successfully compete with their teleost counterparts. Their strategy is to complete their life span quickly (i.e., life in the fast lane). The life history of squids would be a fraction of many of their

teleost counterparts. Their major strategy appears to be a protein-based metabolism that converts energy into growth rather than storage (O'Dor & Webber 1986, Lee 1994, Moltschaniwskyj & Semmens 2000). Their high metabolic rates and growth rates are in fact higher than poikilothermic vertebrates and as high as mammals (Pörtner & Zielinski 1998, Zielinski & Pörtner 2000).

Squid also appear to sustain continued growth by a combination of both an increase in muscle fibre size (hypertrophy) along with continual recruitment of new muscle fibres (hyperplasia) (Moltschaniwskyj 1994, Preuss *et al.* 1997, Pecl & Moltschaniwskyj 1999). While teleost fish have both mechanisms hyperplasia eventually ceases with age.

Cephalopods rapidly digest (Boucher-Rodoni *et al.* 1987) and efficiently use protein, however, they appear to not handle lipids well and it has been recently suggested that the digestive gland is used for dumping excess lipid that cannot be metabolised or

stored (Semmens 1998). Furthermore, the combination of jet pressure locomotion that passes water directly over the gills in association with cutaneous respiration (which might be extremely high in squid; Pörtner 1994, Pörtner & Zielinski 1998) provides a mechanism for efficient oxygen consumption (O'Dor & Hoar 2000). O'Dor & Hoar (2000) have even suggested that the thin mitochondria-rich fin musculature may be independent of the circulatory system. Thus squids appear to use oxygen efficiently despite the limitations of their hemocyanin based respiratory transport system (Hochachka 1994, Pörtner & Zielinski 1998).

We now have clues as to why squids have such short life spans. They may in fact be under biochemical constraints. Zielinski & Pörtner (2000) have recently shown that cephalopods have a low enzymatic antioxidative status despite their high metabolic rate. Their low level of enzymatic antioxidant defense correlates with an increased level of oxidative damage, reflected by very high levels of malondialdehyde (MDA) and lipofuscin which indicates oxidative stress is higher in older specimens. Zielinski & Pörtner (2000) have pointed out that this low antioxidative status is in line with short cephalopod life expectancies. They further pose the question 'why isn't antioxidative defense brought to a higher level to prolong cephalopod life?' Their explanation is that antioxidative protection is set to a level just high enough to allow for a 'sufficient life span'.

Antioxidative defense appears to be an exciting area of future research across a number of squid species with varying life spans and perhaps even within species that show considerable differences in life histories with season or location (e.g., Jackson & Moltschanivskyj 2001a,b). The tradeoff between high oxygen concentrations in tissues to sustain high activity and the need for antioxidant protection could be a factor in cephalopod associations with the oxygen minimum layer (e.g., *Stenoteuthis oualaniensis* in the Arabian Sea, Nesis 1993 and *Gonatus onyx* in the deepsea off California, Hunt & Seibel 2000). It could also be a factor in the ontogenetic descent commonly seen as cephalopods age and mature (e.g. *Moroteuthis ingens* Jackson 1993, 1997, 2001, Jackson *et al.* 2000b, *Gonatus fabricii* Bjørke *et al.* 1997, Arkhipkin & Bjørke 1999, 2000, *Gonatus onyx* Seibel *et al.* 2000, *Beryteuthis magister* Arkhipkin *et al.* 1996, *Galiteuthis glacialis* Nesis *et al.* 1998).

Four important features therefore stand out with regard to mechanisms responsible for squid growth and life span. These are: (1) protein based rapid metabolism and digestion (2) continual recruitment of new muscle fibres (hyperplasia) (3) efficient utilisation of oxygen and (4) low levels of antioxidative defense. These unique features of

squid growth set them apart from their main teleost competitors.

### *Where to from here?*

As world finfish stocks continue to be depleted there is likely to be increasing attention given to cephalopod resources. We thus have a pressing need to understand the dynamics and physiology of squid growth and to develop the essential elements needed for successful squid fishery management (O'Dor 1998, Lipinski 1998, Lipinski *et al.* 1998b).

A critical unknown is whether the traditional ecosystems based on large, slow-growing, late-maturing fishes will ever recover. Worldwide, governments are establishing marine protected areas (MPAs) to assist recovery and maintenance of fished populations. Even if extensive MPAs are established, it is possible that a new dynamic balance of faster growing squids and fishes has already been established. MPAs will provide a safe haven for large, old fishes, but the overall stability of ecosystems managed with this new tool will depend on the interaction of relative production: biomass ratios in protected areas and areas that are still under heavy fishing pressure.

Ultrasonic telemetry is a new and exciting means to study activity and metabolism of both squid (O'Dor *et al.* 2001a) and fish (O'Dor *et al.* 2001a, Webber *et al.* 2000) in real time and to determine essential elements of energetics and ecophysiology *in situ*. Just as Lipinski *et al.* (1998a) has been able to take statolith validation out of the laboratory and into the field environment, remote telemetry allows the researcher to study squid activity and metabolism in the field in a way that is otherwise impossible. Using ultrasonic tags it is possible to telemeter information back on a whole suite of biological parameters of individuals in the field (e.g., O'Dor *et al.* 1994, Dewar *et al.* 1999, Webber *et al.* 1998).

Figure 1 shows an example of parallel studies of squid and fish using radio-acoustic positioning telemetry (RAPT) in an MPA at Lizard Island, Australia (O'Dor *et al.* 2001a). Such studies may not give the complete picture but will certainly represent an important component. While the data presented in Fig. 1 simply shows distribution and movement data, two of the species (one squid and one fish) show movement across the MPA boundary. Such technology provides necessary data for studying the dynamics and interactions of fish and squid in both fished and non-fished areas. Future larger scale studies could utilise the deployment of fixed hydrophone monitors (e.g., Voegeli *et al.* 2001) for tracking movement of individuals over very large distances (10's -1000's of kilometers).

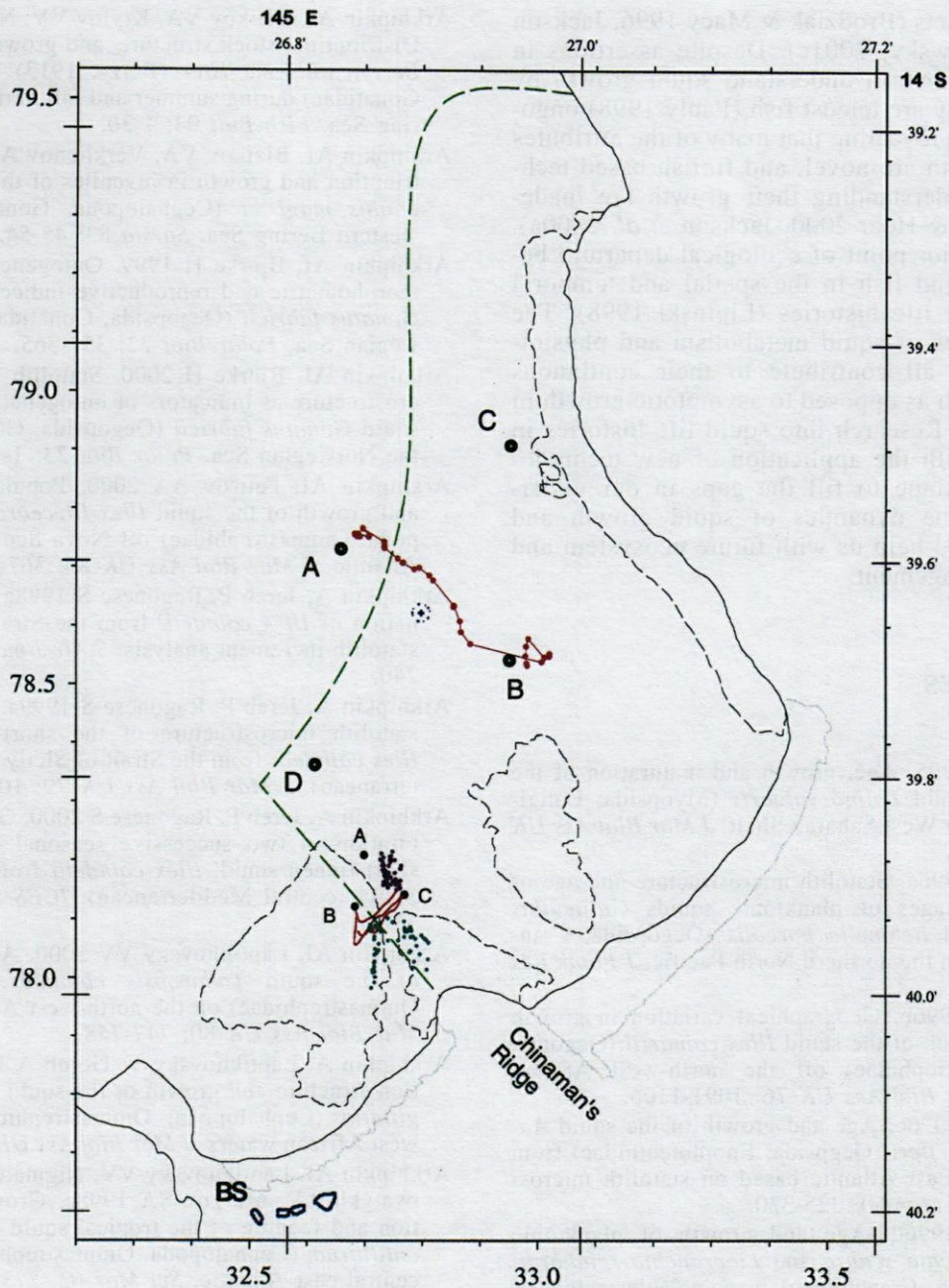


Fig. 1. – RAPT systems deployed in Watson's Bay, Lizard Island, Australia. The map gives both kilometre grid and latitude and longitude references, and the heavy dashed line encloses a no-take MPA zone. The large four-buoy diamond was linked to the base-station (BS) at the Lizard Island Lodge, and produced the illustrated 3h track of the tropical squid *Sepioteuthis lessoniana* crossing the boundary. The smaller triangle recorded territories over 24 h for a stripey *Lutjanus carponotatus* (smaller home range, purple dots) and a coral trout *Plectropomus leopardus* (divided home range, green dots), also showing trans-border movement. The red line is a track of a diver who undertook an underwater survey (From O'Dor *et al.* 2001a).

Currently, much of our understanding regarding squid growth and ecophysiology is imprecise. Even though we know their life histories are short and growth is plastic, we really lack many of the specifics. Continuing work on basic biology and the development of life tables would allow the investigation of age-specific mortality (Wood & O'Dor

2000). We still face difficulties with modelling squid growth due to the extreme plasticity in size-at-age and the rapid response in growth rate due to changes in ambient temperature. Recent work with separating squid samples into seasonal cohorts and using the Schnute model for analysing size-at-age data may be a useful technique for dealing with the



difficult data sets (Brodziak & Macy 1996, Jackson & Moltschaniwskyj 2001c). Despite assertions in the past that we can understand squid growth by pretending they are teleost fish (Pauly 1998) ongoing research is revealing that many of the attributes of squid growth are novel, and finfish based techniques for understanding their growth are inadequate (O'Dor & Hoar 2000, Jackson *et al.* 2000a). There is a major point of ecological departure between squid and fish in the spatial and temporal scales in their life histories (Lipinski 1998). The unique features of squid metabolism and physiology probably all contribute to their continuous form of growth as opposed to asymptotic growth in most teleosts. Research into squid life histories in association with the application of new technologies will continue to fill the gaps in our understanding of the dynamics of squid growth and physiology and help us with future ecosystem and fisheries management.

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