HAL
open science

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

George D Jackson, Ron K O'Dor

To cite this version:

George D Jackson, Ron K O'Dor. TIME, SPACE AND THE ECOPHYSIOLOGY OF SQUID GROWTH, LIFE IN THE FAST LANE. Vie et Milieu / Life & Environment, 2001, pp.205-215. hal-03192511

HAL Id: hal-03192511

https://hal.sorbonne-universite.fr/hal-03192511v1

Submitted on 8 Apr 2021

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

VIE MILIEU, 2001, 51 (4) : 205-215

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

*GEORGE D. JACKSON, RON K. O'DOR**

Institute of Antarctic and Southern Ocean Studies, University of Tasmania, PO Box 252-77, Hobart, Tasmania 7001, Australia
** Census of Marine Life*
CORE, 1755 Massachusetts Ave., Suite 800
Washington, DC 20036-2102, USA
Email: george.jackson@utas.edu.au, rodor@coreocean.org

SQUID GROWTH
STATOLITHS
AGE VALIDATION
METABOLISM
TELEMETRY

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 continuelle de nouvelles fibres (hyperplasie) ; (3) ils utilisent l'oxygène de manière efficace et (4) leur niveau de défenses antioxidantes est bas. La pêche intensive des espèces de Poisson à maturité tardive pourrait avoir modifié de manière irréversible l'équilibre de l'écosytème 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 écosytèmes 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 Yastsu & 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 & Moltschaniwskyj 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
Loligo vulgaris reynaudii	8	Tetracycline staining in field	Lipinski et al. 1998a
Loligo vulgaris	31	Tetracycline staining in culture	Villanueva 2000a
Loligo vulgaris embryos	36	Tetracycline staining in culture	Villanueva 2000b
Loliolus noctiluca	6	Tetracycline staining in culture	Dimmlich & Hoedt 1998
Lolliguncula brevis	43	Tetracycline staining in culture	Jackson et al. 1997
Sepioteuthis lessoniana	5	Alizarin red staining in culture	Balgos & Pauly 1998
Sepioteuthis lessoniana	11	Tetracycline staining in culture	Jackson & Moltschaniwskyj 2001a
Gonatus onyx	4	Counting increments from capture stress check	Arkhipkin & Bizikov 1997
Gonatus borealis	2	Counting increments from capture stress check	Arkhipkin & Bizikov 1997
Gonatus magister	1	Counting increments from capture stress check	Arkhipkin & Bizikov 1997
Galiteuthis phyllura	1	Observing increment from check	Arkhipkin 1996a
Eogonatus tinro	4	Counting increments from capture stress check	Arkhipkin & Bizikov 1997
Berryteuthis magister	88	Comparing statolith increments to gladius increments	Arkhipkin et al. 1996
Berryteuthis magister	60	Comparing increment number to elapsed days between 2 cohorts	Arkhipkin 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* Arkhipkin1995, *Heterololigo bleekeri* 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
Loligo vulgaris	361 (F) 382 (M)	255 (F) 383 (M)	North-west Spain	Some seasonal variation in growth	Rocha & Guerra 1999
Loligo vulgaris	294 (F) 308 (M)	285 (F) 534 (M)	Saharan Bank	Tropical	Raya et al. 1999
Loligo vulgaris	335 (F) 396 (M)	290 (F) 498 (M)	Saharan Shelf	Tropical	Arkhipkin 1995
Loligo vulgaris	~253 (F) ~288 (M)	~308 (F) ~311 (M)	Southern Portugal	Warmwater	Bettencourt et al. 1996
Loligo gahi	366 (F) 339 (M)	~146 (F) ~169 (M)	Patagonian Shelf	Seasonal variation in growth	Hatfield 2000
Loligo opalescens	238(F) 243(M)	~128(F) ~138(M)	California	No differences between males or females	Butler et al. 1999
Loligo pealei	~275 (F) ~295 (M)	~213 (F) ~295 (M)	North-west Atlantic	Growth variable depending on season	Brodziak & Macy 1996
Lolliguncula brevis	172 (F) 150 (M)	72 (F) 61 (M)	Gulf of Mexico	Growth variable depending on season	Jackson et al. 1997
Sepioteuthis lessoniana	173 (F) 224 (M)	276 (F) 256 (M)	Australia, Thailand	Subtropical, tropical, seasonal/geographical differences in growth rates	Jackson & Moltschaniwskyj 2001b
Sepioteuthis lessoniana	~186 (F) ~174(M)	~174 (F) ~212 (M)	Australia	Tropical	Semmens & Moltschaniwskyj 2000
Photololigo sp.	~91	~102	Northeastern Australia	Tropical	Moltschaniwskyj 1995
Photololigo sp. 1	158 (F) 119 (M)	115 (F) 87 (M)	Northwest Shelf of Australia	Tropical	Jackson & Yeatman 1996
Loliolus noctiluca	~250 (F) ~256 (M)	~ 69 (F) ~54 (M)	Eastern Australia ~38°S	Temperate	Dimmlich & Hoedt 1998
Loliolus noctiluca	148 (F) 129 (M)	80 (F) 52 (M)	Eastern Australia ~33°S	Temperate	Jackson & Moltschaniwskyj 2001c
Loliolus noctiluca	121 (F) 107 (M)	54 (F) 61 (M)	Eastern Australia ~19°S	Tropical, seasonal variation in growth	Jackson & Moltschaniwskyj 2001c
Loligo forbesi	514 (F) 480 (M)	322 (F) 400 (M)	North-west Spain	Some seasonal variation in growth	Rocha & Guerra 1999
Abralia trigonura	188 (F) 182 (M)	~36 (F) ~31 (M)	Hawaii	Abundant species in mesopelagic boundary community	Young & Mangold 1994
Abraliopsis pfefferi	154 (F) 127 (M)	33 (F) 25 (M)	Central East Atlantic	Tropical, small, short life span	Arkhipkin 1996c
Ancistrocheirus lesueurii	609 (F) 360 (M)	423 (F) 90 (M)	Central-East Atlantic	Females strikingly larger and older than males	Arkhipkin 1997b
Pterygioteuthis gemmata	77 (F) ~73 (M)	30 (F) ~26 (M)	Central East Atlantic	Tropical, extremely short life span < 3 months	Arkhipkin 1997a
Onychoteuthis banksi	261 (F) 224 (M)	130 (F) 77 (M)	Atlantic, Pacific and Indian Oceans	Females not mature, full life span not known	Arkhipkin & Nigmatullin 1997
Moroteuthis ingens	358 (F) 393 (M)	544 (F) 382 (M)	New Zealand	Sexually dimorphic with females bigger	Jackson 1997
Gonatus fabricii	~644 (F) 654 (M)	~205* (F) 182* (M)	Norwegian Sea	Arctic, suggested 2 year life cycle	Arkhipkin & Bjørke 2000
Berryteuthis magister	473 (M) 479 (F)	295 (M) 369 (F)	Bering Sea	Coldwater	Arkhipkin et al. 1996
Architeuthis	294 (M) 375 (M) 422 (M)	1028 (M) 975 (M) 1084 (M)	Off Ireland	All mature males	Lordan et al. 1998
Illex illecebrosus	~247 (F) ~216 (M)	~280 (F) ~246 (M)	Newfoundland	Growth variable depending on season of hatch	Dawe & Beck 1997
Illex illecebrosus	~198	~205	Nova Scotian shelf		Arkhipkin & Fetisov 2000
Illex coindetii	286 (F) 233 (M)	300 (F) 203 (M)	Western Sahara	2 groups (young 0.5 yr and older ~1yr maturing squid)	Arkhipkin 1996b
Illex coindetii	242 (F) 189 (M)	190 (F) 140 (M)	Sierra Leone	Tropical	Arkhipkin 1996b

Table II. – (*continued*).

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

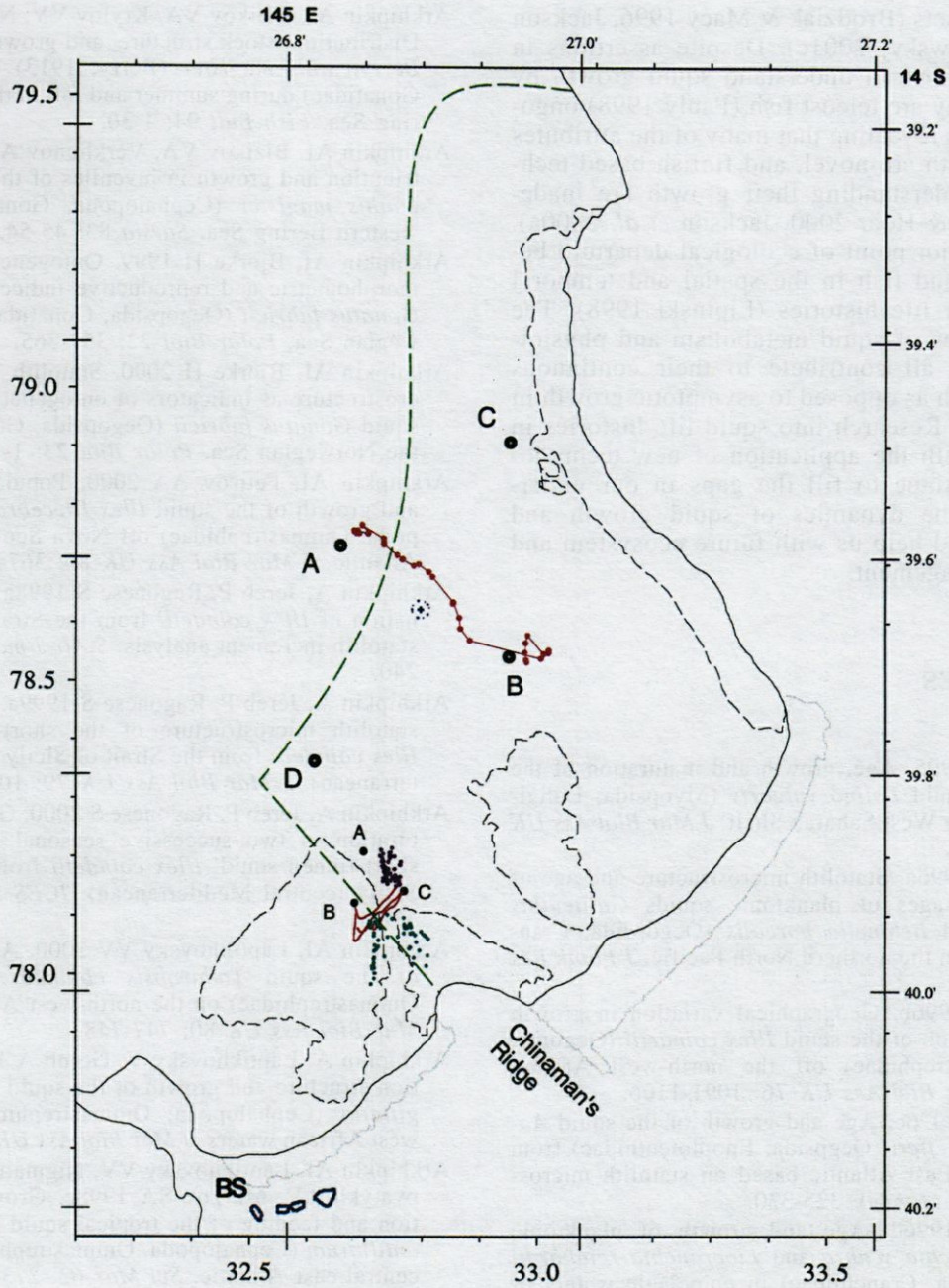

Fig. 1. – RAPT systems deployed in Watson's Bay, Lizard Island, Australia. The map gives both kilometre grid and latitude and longitude references, and the heavy dashed line encloses a no-take MPA zone. The large four-buoy diamond was linked to the base-station (BS) at the Lizard Island Lodge, and produced the illustrated 3h track of the tropical squid *Sepioteuthis lessoniana* crossing the boundry. 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.

REFERENCES

Arkhipkin A 1995. Age, growth and maturation of the European squid *Loligo vulgaris* (Myopsida, Loliginidae) on the West Saharan Shelf. *J Mar Biol Ass UK* 75: 593-604.

Arkhipkin A 1996a. Statolith microstructure and age of early life stages of planktonic squids *Galiteuthis phyllura* and *Belonella borealis* (Oegopsida, Cranchiidae) from the northern North Pacific. *J Plank Res* 18: 123-132.

Arkhipkin A 1996b. Geographical variation in growth and maturation of the squid *Illex coindetii* (Oegopsida, Ommastrephidae) off the north-west African coast. *J Mar Biol Ass UK* 76: 1091-1106.

Arkhipkin AI 1996c. Age and growth of the squid *Aabraliopsis pfefferi* (Oegpsida: Enoploteuthidae) from the Central-East Atlantic based on statolith microstructure. *Sci Mar* 60: 325-330.

Arkhipkin A 1996d. Age and growth of planktonic squids *Cranchia scabra* and *Liocranchia reinhardti* (Cephalopoda, Cranchiidae) in epipelagic waters of the central-east Atlantic. *J Plank Res* 18: 1675-1683.

Arkhipkin AI 1997a. Age of the micronektonic squid *Pterygioteuthis gemmata* (Cephalopoda: Pyroteuthidae) from the central-east Atlantic based on statolith growth increments. *J Moll Stud* 68: 287-290.

Arkhipkin AI 1997b. Age and growth of the mesopelagic squid *Ancistrocheirus lesueurii* (Oegopsida: Ancistrocheiridae) from the central-east Atlantic based on statolith microstructure. *Mar Biol* 129: 103-111.

Arkhipkin AI 2000. Intrapopulation structure of winter-spawned Argentine shortfin squid, *Illex argentinus* (Cephalopoda, Ommastrephidae), during its feeding period over the Patagonian shelf. *Fish Bull* 98: 1-13.

Arkhipkin AI, Bizikov VA 1997. Statolith shape and microstructure in studies in systematics, age and growth in planktonic paralarvae of gonatid squids (Cephalopoda, Oegopsida) from the western Bering Sea. *J Plank Res* 19: 1993-2030.

Arkhipkin AI, Bizikov VA, Krylov VV, Nesis KN 1996. Distribution, stock structure, and growth of the squid *Berryteuthis magister* (Berry, 1913) (Cephalopoda, Gonatidae) during summer and fall in the western Bering Sea. *Fish Bull* 94: 1-30.

Arkhipkin AI, Bizikov VA, Verkhunov AV 1998b. Distribution and growth in juveniles of the squid *Berryteuthis magister* (Cephalopoda, Gonatidae) in the western Bering Sea. *Sarsia* 83: 45-54.

Arkhipkin AI, Bjørke H 1999. Ontogenetic changes in morphometric and reproductive indices of the squid *Gonatus fabricii* (Oegopsida, Gonatidae) in the Norwegian Sea. *Polar Biol* 22: 357-365.

Arkhipkin AI, Bjørke H 2000. Statolith shape and microstructure as indicators of ontogenetic shifts in the squid *Gonatus fabricii* (Oegopsida, Gonatidae) from the Norwegian Sea. *Polar Biol* 23: 1-10.

Arkhipkin AI, Fetisov AA 2000. Population structure and growth of the squid *Illex Illecebrosus* (Cephalopoda: Ommastrephidae) off Nova Scotia, north-west Atlantic. *J Mar Biol Ass UK* 80: 367-368.

Arkhipkin A, Jereb P, Ragonese S 1998a. Age determination of *Illex coindetii* from the Strait of Sicily by statolith increment analysis. *S Afr J mar Sci* 20: 233-240.

Arkhipkin A, Jereb P, Ragonese S 1999a. Checks in the statolith microstructure of the short-finned squid, *Illex coindetii* from the Strait of Sicily (central Mediterranean). *J Mar Biol Ass UK* 79: 1091-1096.

Arkhipkin A, Jereb P, Ragonese S 2000. Growth and maturation in two successive seasonal groups of the short-finned squid, *Illex coindetii* from the Strait of Sicily (central Mediterranean). *ICES J Mar Sci* 57: 31-41.

Arkhipkin AI, Laptikhovsky VV 2000. Age and growth of the squid *Todaropsis eblanae* (Cephalopoda: Ommastrephidae) on the north-west African Shelf. *J Mar Biol Ass UK* 80: 747-748.

Arkhipkin A, Laptikhovsky V, Golub A 1999b. Population structure and growth of the squid *Todarodes sagittatus* (Cephalopoda: Ommastrephidae) in north-west African waters. *J Mar Biol Ass UK* 79: 467-477.

Arkhipkin AI, Laptikhovsky VV, Nigmatullin CM, Bespyatykh AV, Murzov SA 1998c. Growth, reproduction and feeding of the tropical squid *Ornithoteuthis antillarum* (Cephalopoda, Ommastrephidae) from the central-east Atlantic. *Sci Mar* 62: 273-288.

Arkhipkin AI, Nigmatullin CM 1997. Ecology of the oceanic squid *Onychoteuthis banksi* and the relationship between the genera *Onychoteuthis* and *Chaunoteuthis* (Cephalopoda: Onychoteuthidae). *J Mar Biol Ass UK* 77: 839-869.

Arkhipkin AI, Silvanovich NV 1997. Age, growth and maturation of the squid *Martialia hyadesi* (Cephalopoda, Ommastrephidae) in the south-west Atlantic. *Antarctic Sci* 9: 373-380.

Balgos MC, Pauly D 1998. Age and growth of the squid *Sepioteuthis lessoniana* in N. W. Luzon, Philippines. *S Afr J mar Sci* 20: 449-452.

Bettencourt V, Coelho L, Andrade JP, Guerra A 1996. Age and growth of the squid *Loligo vulgaris* off the south coast of Portugal, using statolith analysis. *J Moll Stud* 62: 359-366.

Bjørke H, Hansen K, Sundt RC 1997. Egg masses of the squid *Gonatus fabricii* (Cephalopoda, Gonatidae)

caught with pelagic trawl off northern Norway. *Sarsia* 82: 149-152.

Boucher-Rodoni R, Boucaud-Camou E, Mangold K 1987. Feeding and digestion. *In* Cephalopod Life Cycles, Vol 2, Boyle PR Ed, Academic Press: 85-108.

Bower JR 1996. Estimated paralarval drift and inferred hatching sites for *Ommastrephes bartramii* (Cephalopoda: Ommastrephidae) near the Hawaiin Archipelago. *Fish Bull* 94: 398-411.

Brodziak JKT, Macy WK 1996. Growth of long-finned squid, *Loligo pealei*, in the northwest Atlantic. *Fish Bull* 94: 212-236.

Butler J, Fuller D, Yaremko M 1999. Age and growth of market squid (*Loligo opalescens*) off California during 1998. Calif Coop Fish Invst Repts 40: 191-195.

Caddy JF, Rodhouse PG 1998. Cephalopod and groundfish landings: evidence for ecological change in global fisheries? *Rev Fish Biol Fisheries* 8: 431-444.

Chotiyaputta C 1997. Distribution, abundance, reproductive biology, age and growth of *Loligo chinensis* and *Loligo duvauceli* in the western Gulf of Thailand. *In* Developing and sustaining world fisheries resources, the state of science and management, Hancock DA, Smith DC, Grant A & Beumer JP Eds, CSIRO: 614-619.

Dawe EG, Beck PC 1997. Population structure, growth, and sexual maturation of short-finned squid (*Illex illecebrosus*) at Newfoundland. *Can J Fish Aquat Sci* 54: 137-146.

Dewar H, Deffenbaugh M, Thurmond G, Lashkari K, Block BA 1999. Development of an acoustic telemetry tag for monitoring electromyograms in free-swimming fish. *J Exp Biol* 202: 2693-2699.

Dimmlich WF, Hoedt FE 1998. Age and growth of the myopsid squid *Loliolus noctiluca* in Western Port, Victoria, determined from statolith microstructure analysis. *J Mar Biol Ass UK* 78: 577-586.

Durhlotz MD, Lipinski MR 2000. Influence of temperature on the microstructure of statoliths of the thumbstall squid *Lolliguncula brevis*. *Mar Biol* 136: 1029-1037.

Estácio S, Goncalves J, Porteiro F, Andrade JP 1999. Comparison of fluorescent bands during staining of statoliths of the squid *Loligo forbesi* (Cephalopoda: Loliginidae). *J Moll Stud* 65: 374-377.

Forsythe JW 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 RK & Kubodera T Eds, Tokai University Press: 133-143.

Forsythe JW, Walsh LS, Turk PE, Lee PG 2001. Impact of temperature on juvenile growth and age at first egg-laying of the Pacific reef squid *Sepioteuthis lessoniana* reared in captivity. *Mar Biol* 138: 103-112.

González AF, Castro BG, Guerra A 1996. Age and growth of the short-finned squid *Illex coindetii* in Galician waters (NW Spain) based on statolith analysis. *ICES J Mar Sci* 53: 802-810.

González A, Dawe E, Beck P, Perez J 2000. Bias associated with statolith-based methodologies for ageing squid: a comparative study on *Illex illecebrosus* (Cephalopoda: Ommastrephidae). *J Exp Mar Biol Ecol* 244: 161-180.

González AF, Macy WK 111, Guerra A 1998. Validation of a semi-automatic image analysis system to age squids and its application to age *Illex coindetii* statoliths. *ICES J Mar Sci* 55: 535-544.

González AF, Rodhouse PG 1998. Fishery biology of the seven star flying squid *Martialia hyadesi* at South Georgia during winter. *Polar Biol* 19: 231-236.

González AF, Trathan PN, Yau C, Rodhouse PG 1997. Interactions between oceanography, ecology and fishery biology of the ommastrephid squid *Martialia hyadesi* in the South Atlantic. *Mar Ecol Prog Ser* 152: 205-215.

Hatfield E 2000. Do some like it hot? Temperature as a possible determinant of variability in the growth of the Patagonian squid, *Loligo gahi* (Cephalopoda: Loliginidae). *Fish Res* 47: 27-40.

Hochachka PW 1994. Oxygen efficient design of cephalopod muscle metabolism. *Mar Behav Physiol* 25: 61-67.

Hunt JC, Seibel BA 2000. Life history of *Gonatus onyx* (Cephalopoda: Teuthoidea): ontogenetic changes in habitat, behavior and physiology. *Mar Biol* 136: 543-552.

Jackson GD 1990. Age and growth of the tropical nearshore Loliginid squid *Sepioteuthis lessoniana* determined from statolith growth ring analysis. *Fish Bull* 88: 113-118.

Jackson GD 1993. Growth zones within the statolith microstructure of the deepwater squid *Moroteuthis ingens* (Cephalopoda: Onychoteuthidae): evidence for a habitat shift. *Can J Fish Aquat Sci* 50: 2366-2374.

Jackson GD 1994. Application and future potential of statolith increment analysis in squids and sepioids. *Can J Fish Aquat Sci* 51: 2612-2625.

Jackson GD 1997. Age, growth and maturation of the deepwater squid *Moroteuthis ingens* (Cephalopoda: Onychoteuthidae) in New Zealand waters. *Polar Biol* 17: 268-274.

Jackson GD 1998. Research into the life history of *Loligo opalescens*: where to from here? *CalCOFI Rep* 39: 101-107.

Jackson GD 2001. Confirmation of winter spawning of *Moroteuthis ingens* (Cephalopoda: Onychoteuthidae) in the Chatham Rise region of New Zealand. *Polar Biol* 24: 97-100.

Jackson GD, Alford RA, Choat. JH 2000a. Can squid populations be analyzed using standard fishery length-based techniques? *ICES J Mar Sci* 57: 948-954.

Jackson GD, Arkhipkin AI, Bizikov VA, Hanlon RT 1993. Laboratory and field corroboration of age and growth from statoliths and gladii of the loliginid squid *Sepioteuthis lessoniana* (Mollusca: Cephalopoda). *In* Recent advances in cephalopod fisheries biology, Okutani T, O'Dor RK & Kubodera T Eds, Tokai University Press: 189-199.

Jackson GD, Choat JH 1992. Growth in tropical cephalopods: an analysis based on statolith microstructure. *Can J Fish Aquat Sci* 49: 218-228.

Jackson GD, Forsythe JW, Hixon RF, Hanlon RT 1997. Age, growth, and maturation of *Lolliguncula brevis* (Cephalopoda: Loliginidae) in the northwestern Gulf of Mexico with a comparison of length-frequency versus statolith age analysis. *Can J Fish Aquat Sci* 54: 2907-2919.

Jackson GD, Moltschaniwskyj NA 1999. Analysis of precision in statolith derived age estimates of the tro-

pical squid *Photololigo* (Cephalopoda: Loliginidae). *ICES J Mar Sci* 56: 221-227.

Jackson GD, Moltschaniwskyj NA 2001a. The influence of ration level on growth and statolith increment width of the tropical squid *Sepioteuthis lessoniana* (Cephalopoda: Loliginidae): an experimental approach. *Mar Biol* 138: 89-825.

Jackson GD, Moltschaniwskyj NA 2001b. Spatial and temporal variation in growth rates and maturity in the Indo-Pacific squid *Sepioteuthis lessoniana* (Cephalopoda: Loliginidae). *Mar Biol* (in press)

Jackson GD, Moltschaniwskyj NA 2001c. Temporal variation in growth rates and reproductive parameters in the small near-shore tropical squid, *Loliolus noctiluca*; is cooler better? *Mar Ecol Prog Ser* 218: 167-177.

Jackson GD, Shaw AGP, Lalas C 2000b. Distribution and biomass of two squid species off southern New Zealand: *Nototodarus sloanii* and *Moroteuthis ingens*. *Polar Biol* 23: 699-705.

Jackson GD, Wadley VA 1998. Age growth, and reproduction of the tropical squid *Nototodarus hawaiiensis* (Cepahlopoda: Ommastrephidae) off the North West Slope of Australia. *Fish Bull* 96: 779-787.

Jackson GD, Yeatman J 1996. Variation in size and age at maturity in *Photololigo* (Mollusca: Cephalopoda) from the northwest shelf of Australia. *Fish Bull* 94: 59-65.

Kinoshita A 1989. Age and growth of the l oliginid squid, *Heterloligo bleekeri*. *Bull Seikai Reg Fish Res Lab* 67: 59-69.

Lee PG 1994. Nutrition of cephalopods: fueling the system. *Mar Behav Physiol* 25: 35-51.

Lee PG, Turk PE, Yang WT, Hanlon RT 1994. Biological characteristics and biomedical applications of the squid *Sepioteuthis lessoniana* cultured through multiple generations. *Biol Bull* 186: 328-341.

Lipinski MR 1991. Scanning electron microscopy (SEM) and chemical treatment. *In* Squid age determination using statoliths, Jereb P, Ragonese S & Boletzky S v Eds, Proceed intern workshop Istituto di Tecnologia della Pesca e del Pescato (ITPP-CNR), Mazara del Vallo, Italy, 9-14 October 1989, N.T.R.–I.T.P.P. Spec Publ no 1: 97-107.

Lipinski MR 1998. Cephalopod life cycles: patterns and exceptions. S *Afr J mar Sci* 20: 439-447.

Lipinski MR, Durholtz MD, Underhill LG. 1998a. Field validation of age readings from the statoliths of chokka squid (*Loligo vulgaris reynaudii* d'Orbigny, 1845) and an assessment of associated errors. *ICES J Mar Sci* 55: 240-257.

Lipinski MR, Butterworth DS, Augustyn CJ Brodziak JKT, Christy G, Des Clers S, Jackson GD, O'Dor RK, Pauly D, Purchase LV, Roberts MJ, Roel BA, Sakurai Y, Sauer WHH 1998b. 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. *S Afr J mar Sci* 20: 463-469.

Lordan C, Collins MA, Key L, Browne ED 2001. The biology of the ommastrephid squid, *Todarodes sagittatus*, in the north-east Atlantic. *J Mar Biol Ass UK* 81: 299-306.

Lordan C, Collins MA, Perales-Raya C 1998. Observations on morphology, age and diet of three *Architeuthis* caught off the west coast of Ireland in 1995. *J Mar Biol Ass UK* 78: 9003-9917.

Macy WK111, Brodziak JKT 2001. Seasonal maturity and size at age of *Loligo pealeii* in waters of southern New England. *ICES J Mar Sci* 58: 852-864.

Moltschaniwskyj NA 1994. Muscle tissue growth and muscle fibre dynamics in the tropical loliginid squid *Photololigo* sp. (Cephalopoda Loliginidae). *Can J Fish Aquat Sci* 51: 830-835.

Moltschaniwskyj NA 1995. Changes in shape associated with growth in the loliginid squid *Photololigo* sp.: a morphometric approach. *Can J Zool* 73: 1335-1343.

Moltschaniwskyj NA, Semmens JM 2000. Limited use of stored energy reserves for reproduction by the tropical loliginid squid *Photololigo* sp. *J Zool Lond* 251: 307-313.

Murphy E, Rodhouse PG 1999. Rapid selection effects in a short-lived semelparous squid species exposed to exploitation: inferences from the optimisation of life-history functions. *Evol Ecol* 13: 517-537.

Nabhitabhata J 1995. The culture of cephalopods: commercial scale attempts in Thailand. *In* Aquaculture towards the 21st century, Nambiar KPP & Singh T Eds, Proceed Infofish-Aquatech 94, Inter conf on aquaculture Colombo, Sri Lanka, 29-31 August 1994, Infofish 1995: 138-144.

Nabhitabhata J 1996. Life cycle of cultured big fin squid, *Sepioteuthis lessoniana* Lesson. *Phuket Marine Biological Centre Spec Publi* 16: 83-95.

Nesis KN 1993. Population structure of oceanic ommastrephids, with particular reference to *Sthenoteuthis oualaniensis*: a review. *In* Recent advances in fisheries biology, Okutani T, O'Dor RK & Kubodera T Eds, Tokai University press: 375-383.

Nesis KN, Nigmatullin ChM, Nikitina IV 1998. Spent females of deepwater squid *Galiteuthis glacialis* under the ice at the surface of the Weddell Sea (Antarctic). *J Zool Lond* 244: 185-200.

Nigmatullin CM, Arkhipkin AI, Sabirov RM 1995. Age, growth and reproductive biology of diamond-shaped squid *Thysanoteuthis rhombus* (Oegopisida: Thysanoteuthidae). *Mar Ecol Prog Ser* 124: 73-87.

O'Dor RK 1998. Can understanding squid life-history strategies and recruitment improve management? *S Afr J mar Sci* 20: 193-20.

O'Dor RK, Aitken JP, Babcock RC, Bolden SK, Seino S, Zeller DD, Jackson GD 2001a. Using radio-acoustic positioning and telemetry (RAPT) to define and assess marine protected areas (MPA's). *In* Electronic tagging and tracking in marine fisheries, Vol 1, Sibert J & Nielsen J Eds, Kluwer Academic Press: 147-168.

O'Dor R, Adamo SA, Andrade Y, Finn J, Hanlon RT, Jackson. GD 2001b. Currents as environmental constraints on the behavior, energetics and distribution of cephalopods. *Bull Mar Sci* (in press).

O'Dor, RK, Hoar JA, Webber DM, Carey FG, Tanaka S, Martins H, Porteiro FM 1994. Squid (*Loligo forbesi*) performance and metabolic rates in nature. *Mar Fresh Behav Physiol* 25: 163-177.

O'Dor RK, Webber DM 1986. The constraints on cephalopods: why squid aren't fish. *Can J Zool* 64: 1591-160.

O'Dor R, Hoar J 2000. Does geometry limit squid growth? *ICES J Mar Sci* 57: 8-14.

Pauly D 1998. Why squid, though not fish, may be better understood by pretending they are. *S Afr J mar Sci* 20: 47-58.

Pauly D, Christensen V 1995. Primary production required to sustain global fisheries. *Nature* 374: 255-257.

Pecl G 2001 Flexible reproductive strategies in tropical and temperate *Sepioteuthis* squids. *Mar Biol* 138: 93-101.

Pecl G, Moltschaniwskyj N 1999. Somatic growth processes: how are they altered in captivity? *Proc R Soc Lond B* 266: 1133-1139.

Pörtner HO 1994. Coordination of metabolism, acid-base regulation and haemocyanin function in cephalopods. *Mar Fresh Behav Physiol* 25: 131-148.

Pörtner HO, Zielinski S 1998. Environmental constraints and the physiology of performance in squids. *S Afr J mar Sci* 20: 207-221.

Preuss T, Lebaric ZN, Gilly WF 1997. Post-hatching development of circular mantle muscles in the squid *Loligo opalescens*. *Biol Bull* 192: 375-387.

Raya CP, Balguerías E, Fernández-Núñez MM, Pierce GJ 1999. On reproduction and age of the squid *Loligo vulgaris* from the Saharan Bank (north-west African coast). *J Mar Biol Ass UK* 79: 111-120.

Rocha F, Guerra A 1999. Age and growth of two sympatric squid *Loligo vulgaris* and *Loligo forbesi*, in Galician waters (north-west Spain). *J Mar Biol Ass UK* 79: 697-707.

Rodhouse PG, Hatfield EMC 1990. Age determination in squid using statolith growth increments. *Fish Res* 8: 323-334.

Seibel BA, Hochberg FG, Carlini DB 2000. Life history of *Gonatus onyx* (Cephalopoda: Teuthoidea): deep sea spawning and post-spawning egg care. *Mar Biol* 137: 519-526.

Semmens J 1998. An examination of the role of the digestive gland of two loliginid squids, with respect to lipid: storage or excretion? *Proc R Soc Lond* B 265: 1685-1690.

Semmens JM, Moltschaniwskyj NA 2000. An examination of variable growth in the loliginid squid *Sepioteuthis lessoniana*: a whole animal and reductionist approach. *Mar Ecol Prog Ser* 193: 135-141.

Sánchez P 1995. Age and growth of *Illex coindetii*. *ICES Mar Sci Symp* 199: 441-444.

Segawa S 1987. Life history of the oval squid, *Sepioteuthis lessoniana* in Kominato and adjacent waters Central Honshu, Japan. *Tokyo Univ Fisheries* 74 2: 67-105.

Tsuchiya M 1982. On the culture of the squid, *Sepioteuthis lessoniana* Lesson (Loliginidae), from hatching to the whole life in Iriomote Island, Okinawa. *Bull Inst Oceanic Res Develop*, Tokai Univ 4.

Uozumi Y 1998. Fishery biology of arrow squids, *Nototodarus gouldi* and *N. sloanii*, in New Zealand waters. *Bull Nat Res Inst Far Seas Fish* 35: 1-111.

Villanueva R 2000a. Effect of temperature on statolith growth of the European squid *Loligo vulgaris* during early life. *Mar Biol* 136: 449-460.

Villanueva R 2000b. Differential increment deposition rate in embryonic statoliths of the loliginid squid *Loligo vulgaris*. *Mar Biol* 37: 161-168.

Voegeli FA, Smale MJ, Webber DM, Andrade Y, O'dor RK 2001. Ultrasonic telemetry, tracking and automated monitoring technology for sharks. *Env Biol Fish* 60: 267-281.

Webber DM, Boutilier RG, Kerr SR 1998. Cardiac output as a predictor of metabolic rate in cod *Gadus morhua*. *J Exp Biol* 201: 2779-2789.

Webber DM, Voegeli FA, Smale MJ 2000. The development of differential pressure techniques to measure swimming speed in fish. *In* Biotelemetry 15: Proceed 15th Intern Sympos on Biotelemetry, Juneau, Alaska, USA Eiler J, Alcorn DJ & Neuman MR Eds, Intern Soc on Biotelemetry: 212-221.

Wood JB, O'Dor RK 2000. Do larger cephalopods live longer? Effects of temperature and phylogeny on interspecific comparisons of age and size at maturity. *Mar Biol* 136: 91-99.

Yatsu A 2000. Age estimation of four oceanic squids, *Ommastrephes bartramii*, *Dosidicus gigas*, *Sthenoteuthis oualaniensis*, and *Illex argentinus* (Cephalopoda, Ommastrephidae) based on statolith microstructure. *Japan Agri Res Quart* 34: 75-80.

Yatsu A, Midorikawa S, Shimada T, Uozumi Y 1997. Age and growth of the neon flying squid, *Ommastrephes bartrami*, in the North Pacific Ocean. *Fish Res* 29: 257-270.

Yatsu A, Mochioka N, Morishita K, Toh H 1998. Strontium/calcium ratios in statoliths of the neon flying squid, *Ommastrephes bartrami* (Cephalopoda), in the North Pacific Ocean. *Mar Biol* 131: 275-282.

Yatsu A, Mori J 2000. Early growth of the autumn cohort of neon flying squid, *Ommastrephes bartramii*, in the North Pacific Ocean. *Fish Res* 45: 189-194.

Young RE, Mangold KM 1994. Growth and reproduction in the mesopelagic-boundary squid *Abralia trigonura*. *Mar Biol* 119: 413-421.

Zielinski S, Pörtner HO 2000. Oxidative stress and antioxidative defense in cephalopods: a function of metabolic rate or age? *Comp Biochem Physiol B* 125: 147-160.

Reçu le 28 juillet 2001; received July 28, 2001.
Accepté le 26 septembre 2001; accepted September 26,2001