

# Interannual variability in size structure, age, and growth of jumbo squid (*Dosidicus gigas*) assessed by modal progression analysis

Friedemann Keyl<sup>1\*</sup>, Juan Argüelles<sup>2</sup>, and Ricardo Tafur<sup>2</sup>

<sup>1</sup>Leibniz Centre for Tropical Marine Ecology (ZMT), Fahrenheitstr. 6, 28359 Bremen, Germany

<sup>2</sup>Instituto del Mar del Peru (IMARPE), Esquina Gamarra y General Valle s/n, Chucuito, Callao, Peru

\*Corresponding Author: tel: +49 421 238 0070; fax: +49 421 238 0030; e-mail: [keyl@uni-bremen.de](mailto:keyl@uni-bremen.de).

Keyl, F., Argüelles, J., and Tafur, R. 2011. Interannual variability in size structure, age, and growth of jumbo squid (*Dosidicus gigas*) assessed by modal progression analysis. – ICES Journal of Marine Science, 68: 507–518.

Received 11 May 2010; accepted 8 October 2010; advance access publication 11 November 2010.

A range of growth rates, longevity, maximum size, and number of annual cohorts have been documented for jumbo squid (*Dosidicus gigas*). Genetic and phenotypic plasticity have been mentioned as possible sources of the differences in maximum sizes. Here, a large dataset on length frequencies derived from the industrial jig fishery for the species off Peru from 1991 to 2007 was corrected for observation bias introduced by the fishing gear and used to analyse growth-related parameters by modal progression analysis (MPA). Mean growth rates of 33 cohorts varied interannually (11–44 mm month<sup>-1</sup>), as did longevity (11.1–32.1 months) and mean maximum size (273–1024 mm). Intra-annual difference in growth parameters was not significant. The number of cohorts per year fluctuated between 0 and 6. Fast-growing cohorts with medium longevity and large terminal size were found during moderately cool periods, and long-lived, slow-growing cohorts with small terminal size during extreme ecosystem conditions (*El Niño* and *La Niña*). The application of MPA to cephalopod populations has been rejected before, but the results presented suggest that a modified approach is appropriate if it allows for varying growth parameters and includes a correction for observation bias.

**Keywords:** environmental conditions, growth parameters, jumbo squid, modal progression analysis, Peru, plasticity.

## Introduction

The nerito-oceanic jumbo squid (*Dosidicus gigas*), an ommastrephid, is an important component of eastern Pacific Ocean ecosystems, of both hemispheres (Field *et al.*, 2007; Rosas-Luis *et al.*, 2008). It sustains a fishery that by landings in 2006 was the 12th largest in the world; the jumbo squid fisheries in the Peruvian exclusive economic zone (EEZ) usually contribute at least one-third of the global landings of the species (<ftp://ftp.fao.org/FI/STAT/summary/a1e.pdf>). The species is caught off Peru by a jig fishery similar to those established for other species of squid worldwide (Hatanaka *et al.*, 1985). Jigs are deployed on a vertical line as a varying number of hook crowns arranged one on top of each other. The jigs show a clear Gaussian-distributed length selectivity according to size and are deployed according to the size of the squid in the vicinity (Nesis, 1983; Rathjen, 1991; JA, unpublished data).

The jumbo squid is a monocyclic species, i.e. it dies after spawning (Rocha *et al.*, 2001), so size-at-maturity and maximum size are linked. Three distinct groups of size-at-maturity resulting in different maximum size have been assumed by some authors in the past (Nesis, 1970, 1983), seemingly restricted to different latitudes of the overall distribution: a group attaining small maximum size in tropical regions, a mid-sized group over the entire distribution, and a group attaining large size in higher latitudes of the distribution, in both hemispheres. The range of sizes of these groups are generally assumed to be 130–340 mm dorsal mantle length (ML), 240–600 mm ML, and >400–1200 mm ML, respectively

(Nigmatullin *et al.*, 2001). In contrast to this hypothesis of spatial distribution, others have documented a temporal distribution of sizes-at-maturity (Bazzino *et al.*, 2007; Argüelles *et al.*, 2008), with varying sizes-at-maturity between two extremes assumed rather than three distinguishable groups of size-at-maturity (Keyl *et al.*, 2008; Tafur *et al.*, 2010).

The origin of the groups has been proposed to be either a phenotypic (Nesis, 1983; Keyl *et al.*, 2008) or a genetic response (Nesis, 1983) to environmental conditions. Temperature (Nesis, 1970, 1983) and food availability, or both, have been suggested as principal factors (Keyl *et al.*, 2008). In our Humboldt Current System (HCS) study area, these two factors are closely related and specific for different water masses. The locations of water masses in the system vary, and their extents depend on basin-scale climate variability. During *El Niño* (EN) events, warmer, less-productive water masses dominate the Peruvian part of the HCS, whereas during *La Niña* (LN) events, cooler water masses prevail (Ayón *et al.*, 2008a; Swartzman *et al.*, 2008). The increased size-at-maturity of *D. gigas* in Peruvian waters since around 2000 (Argüelles *et al.*, 2008) has been suggested to be linked to the cooler water masses with greater availability of food that have dominated the region since then. A smaller size-at-maturity is supposedly linked to less-productive, warmer water masses (Keyl *et al.*, 2008).

The lifespan of all three groups of size-at-maturity has been generally assumed to be 1 year, and only the largest animals of the bigger group are thought to attain an age of two years

**Table 1.** Growth parameters of *D. gigas* from 1981 to 2004 in different areas of the eastern Pacific as obtained by MPA, statolith analysis, and tag-recapture.

Area	Sample date	Longevity	Size (mm)	Growth rate (mm year <sup>-1</sup> )	Method	Source
–	–	1 year	200–350	200–330	MPA, assuming a single annual cohort	Nesis (1970)
		2 years	300–500			
		3–4 years	>500			
GoC	–	2 years	–	700–750	MPA	Ehrhardt <i>et al.</i> (1983)
Outside EEZ Peru and Ecuador	March 1981–February 1984	–	Two size groups	690–735	Statoliths	Arkhipkin and Murzov (1987) <sup>a</sup>
Off Peru	1987–1995	1 year	Two size groups	–	Statoliths	Masuda <i>et al.</i> (1998)
Peruvian EEZ	1991–1994	–	Max. 1000	468 in first and 252 in second years	MPA	Argüelles (1996)
Peruvian EEZ	1992	220/354 d	474/965	786–995	Statoliths	Argüelles <i>et al.</i> (2001)
GoC	1995–1997	386 d	875	827	Statoliths	Markaida <i>et al.</i> (2004)
GoC	1995–2002	2.3–2.8 years <sup>b</sup>	76–960	266–399 <sup>c</sup>	MPA	Nevárez-Martínez <i>et al.</i> (2006)
Central GoC	2002	–	–	383 (365–547)	Tag-recapture	Markaida <i>et al.</i> (2005)
Pacific off Baja California	2004	♀ 433 d	830	♀ 721 <sup>d</sup>	Statoliths	Mejía-Rebollo <i>et al.</i> (2008)
		♂ 391 d	690	♂ 655 <sup>d</sup>		

GoC, Gulf of California, Mexico; EEZ, exclusive economic zone.

<sup>a</sup>Cited in Argüelles *et al.* (2001).

<sup>b</sup>Calculated from K.

<sup>c</sup>Mean growth rate.

<sup>d</sup>Mean growth rate of largest squid.

(Nigmatullin *et al.*, 2001). In that case, growth rates for the three size groups must then differ. Other studies have found that age is related to size (Argüelles *et al.*, 2001), which in turn can be interpreted as equal or similar growth rates for all size classes. Past studies on the topic using data from relatively short periods are here reviewed in an attempt to clarify the situation (Table 1). The methods used were modal progression analysis (MPA) based on length frequency analysis (LFA), analysis of statolith rings, and tag-recapture. The statolith analyses assumed that statolith rings are laid down daily, although the one-mark-per-day-assumption has never been tested for *D. gigas*.

The values for longevity documented previously lie between several months for animals maturing at small ML (Argüelles *et al.*, 2001) and up to 4 years for animals >500 mm (Nesis, 1970). Minimum and maximum growth rates lie between 200 and 995 mm year<sup>-1</sup> (Nesis, 1970, and Argüelles *et al.*, 2001, respectively). A great discrepancy between the results of two methods of age evaluation has been described previously for fish (Morales-Nin 1989a, b; Hammers and Miranda, 1991) and cephalopods (Arkhipkin *et al.*, 2000; references in Jackson *et al.*, 2000). The results of studies on growth of *D. gigas* in general and specifically in the Peruvian HCS are no exception to this. Examples where the results of MPA and otolith/statolith analysis agree do exist, e.g. for *Thysanoteuthis rhombus* (Nigmatullin *et al.*, 1995; Miyahara *et al.*, 2006).

Here, we assume that interannual variability could be a source of inconsistency in previous studies on growth of *D. gigas*. Until now such variability has not been taken into account for the species, so the main objective of the study was to identify cohorts of the Peruvian population of *D. gigas* and determine their growth rate, maximum size, and longevity using data collected in the industrial fishery conducted in the Peruvian EEZ. An attempt is also made to relate the supposed variability to

prevailing environmental conditions to try to understand its origin. Additionally, the possible sources of biases in the frequently described discrepancies between the two methods used for evaluation of age and growth, statolith analysis and the analysis of length frequency data, are discussed.

## Data and methods

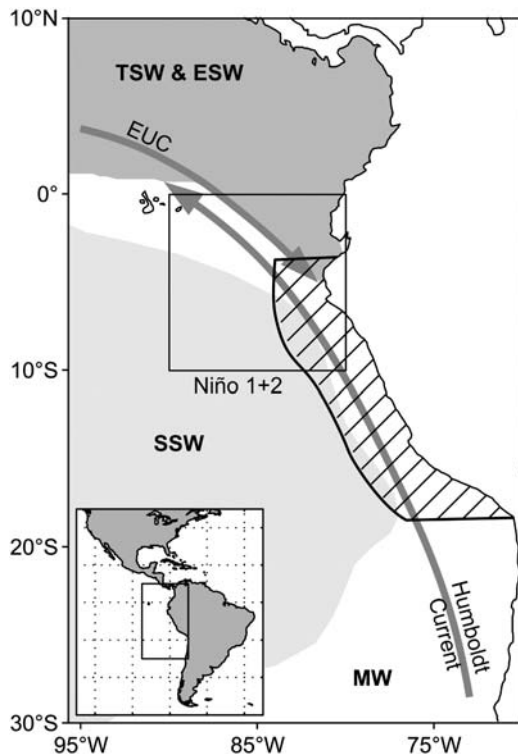
Between 1991 and 2007, the ML of >4.3 million jumbo squid was measured to the nearest centimetre aboard fishing vessels by on-board staff for the IMARPE monitoring programme of the industrial *D. gigas* fishery in the Peruvian EEZ (Figure 1). Data for 1998 were taken during IMARPE research cruises. Records from the entire Peruvian EEZ were pooled to prevent errors caused by migration from influencing the MPA, because virtually all the relevant migration of the stock would be covered inside this area. All length frequencies taken during a calendar month were integrated to obtain a series of 175 months of length frequency grouped into 10-mm size classes.

The raw length frequencies per month were brought to percentages and plotted in a Hovmöller plot as a means of data overview, with monthly values translated to a colour scheme and each column representing 1 month (Figure 2). To decompose the monthly length frequency distributions, a multiple-cohort model with the Gaussian distribution and observation bias correction was used:

$$\text{Occurrence ML} = \exp^{-(\text{ML}-a/b)^2} \sum_{i=1}^n c_i \exp^{-(\text{ML}-d_i/e_i)^2},$$

where *a* through *e* are the parameters determining the Gaussian functions that describe individual cohorts and the observation function (the first term of the equation). The latter corrects the

observation bias introduced via the size-selective jigs by altering the observed length frequencies to the assumed underlying real modes, as shown in the example in Figure 3. If an observation bias was not identified, that term of the model was simply set to 1. Models with different numbers of modes (i.e. numbers of cohorts present) with and without bias were fitted to the data for each month. The resulting models for a specific month were carefully compared using correlation-coefficient and error-distribution plots to identify the best model. The resulting modes represent the underlying cohorts in each month. The LFA algorithm was programmed in Matlab.

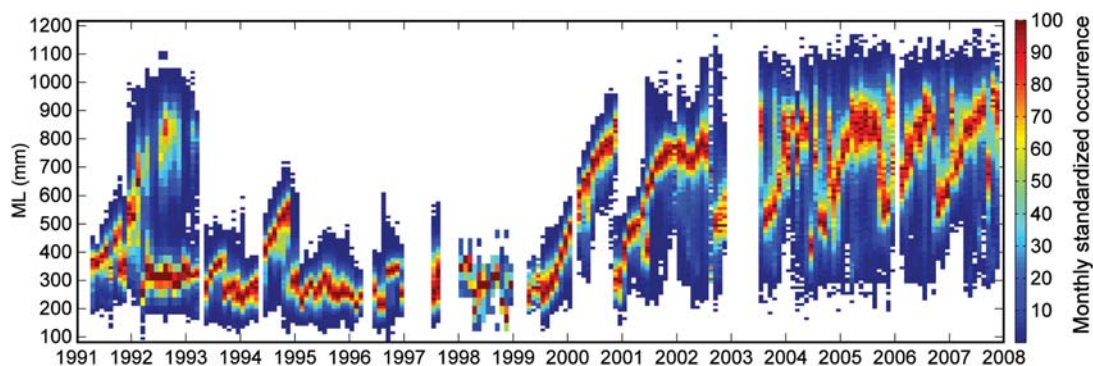


**Figure 1.** The study area in the Peruvian EEZ (hatched) showing the Humboldt Current and the Equatorial Under Current (EUC) as well as the general mean location of the main water masses and the EN 1 + 2 monitoring area. TSW, Tropical Surface Waters; ESW, Equatorial Surface Waters; SSW, Subtropical Surface Waters; MW, mixed water.

In MPA, the maximum values of each mode were overlaid on a Hovmöller plot that was recalculated from the modes obtained by LFA. It had been intended to assign all modes to one cohort by considering their maxima and their position relative to other modes and cohorts already identified, so when cohorts and modes could not be assigned unambiguously or when fewer than four modes were found for a specific cohort, they were counted but not considered in the analysis of growth parameters.

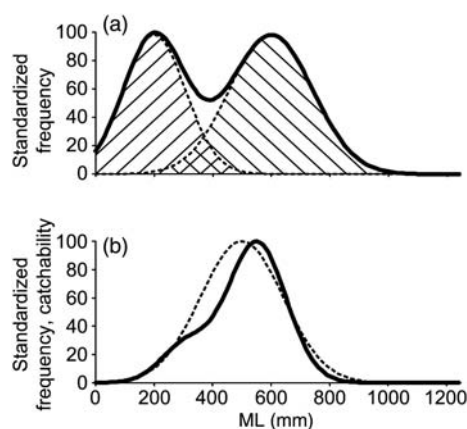
In MPA, the von Bertalanffy growth function (VBGF) is often used. However, the adoption of a VBGF without considering spawning processes (and other processes) has been criticized (Day and Taylor, 1997). Existing studies on the growth function of cephalopods are not consistent, and exponential, linear, and asymptotic functions with and without seasonal oscillation have been proposed (e.g. Masuda *et al.*, 1998; Pauly, 1998; Semmens *et al.*, 2004; Miyahara *et al.*, 2006). For adult squid, non-asymptotic (Jackson *et al.*, 2000), linear, or quasi-linear growth has been postulated or can be identified in the literature (e.g. Masuda *et al.*, 1998; Yatsu, 2000). This has been attributed to the pedomorphic (subadult maturation) life history of cephalopods (Rodhouse, 1998; Hatfield, 2000; Figure 4a). For Peruvian jumbo squid, the modes do not progress according to an asymptotic VBGF, but indicate linear growth (Figure 2). Taken with the exponential growth proposed for ommastrephid paralarvae (Yatsu, 2000) and senescence, i.e. death shortly after the completion of the first spawning cycle and before reaching the asymptotic part of the VBGF (Pauly, 1998), a pseudo-linear growth function would result for coleoid cephalopods (Figure 4b), similar to the basic general growth model (BGM) proposed by Lipiński (2002).

The data used here provide very little information on animals smaller than ML ~150 mm, so neither asymptotic growth nor seasonal variation is identifiable from the data (Figure 2). Therefore, to analyse the modal progression of cohorts, a simple linear regression corresponding to the second-most important growth phase of the Lipiński (2002) BGM was applied to the identified maxima of the modes of a cohort. The mean modal progression of a cohort is equal to the slope of the regression line resulting from the maxima of all modes belonging to that cohort. The mean modal progression of a cohort retrieved from the spatially pooled length frequency is assumed to be equal to the actual mean growth rate of a specific cohort, and both are used synonymously hereafter. Note, however, that the results from MPA cannot give direct information on the growth parameters of individual squid.



**Figure 2.** The Hovmöller plot of the standardized monthly occurrence of *D. gigas* in 10-mm ML classes (maximum value per month, 100).





**Figure 3.** A hypothetical example of observation bias in a length frequency distribution; (a) real cohorts (dotted line enclosing hatched areas) and the resulting real length distribution (black line); (b) the observed length frequency distribution (black line) of the real cohorts in (a) resulting from size selectivity of a jig gear (dotted line).

The maximum size of a cohort is equal to the mean size of its largest mode. Ignoring exponential growth of paralarvae (Yatsu, 2000), the extrapolation of the regression to  $ML = 0$  results in the latest possible hatching date of each cohort. The minimum age of a cohort was calculated by subtracting the calculated hatching date from the month of its largest. This procedure assures a one-sided error and consequent underestimation of the longevity of all cohorts. Longevity estimated in this manner never exceeds the real longevity, which cannot be guaranteed using an exponential growth function for early life stages without more information. The number of cohorts recruiting to a fishery in the succeeding 12 months was determined for each month.

## Results

### Growth parameters of the cohorts identified

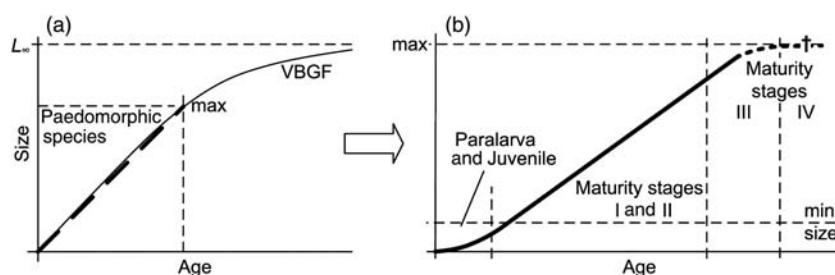
In all, 50 cohorts were identified in the period from April 1991 to December 2007, but growth parameters could only be estimated for 33 of them. These 33 cohorts do not show a consistent picture with respect to its sequence, terminal size, or mean growth rate (Figures 5 and 6; Table 2). Three main periods with similar growth parameters can be identified: (i) up to about 1994, (ii) 1995–1998, and (iii) post-1998. The mean growth rates of the cohorts shown in Figure 6a illustrate these periods clearly, but they can also be identified in the maximum size distributions (Figure 6b). In early 1992, during the first period, mean growth

rates suddenly dropped to values similar to those of the second period. Longevity in the first period was continuously decreasing, and at first appears to have been relatively independent of final size. The shortest lifespan of just over 11 months (cohort 19) was at the end of the first period and just before the decrease in the mean growth rate and the change to an extended lifespan. It is of note that the subsequent cohorts of the second period, which all apparently lived 2–3 times longer, rarely attained greater length than that cohort. The longest lifespan of >32 months was calculated for cohort 25, one of the smallest of the cohorts identified here. We reiterate here that estimated longevity is the minimum age of the cohorts determined by back-calculation and assuming linear growth. The maximum size of the cohorts is also variable, with clear steps in 1991 and 1998 (Figure 6b, Table 2). Cohorts with maximum sizes from 274 to 1024 mm were identified, and there has been a gradual increase in maximum cohort size since 2000. Cohorts that attained large size ( $\geq 675$  mm) were hatched in 1990 and after 1998, whereas cohorts that remained relatively small ( $\leq 386$  mm) were hatched from 1992 to 1998. An exception to this statement are two cohorts from 1993 that attained a maximum sizes of 562 and 450 mm and one cohort that attained just 425 mm post-1998, when other cohorts attained sizes well above 600 mm.

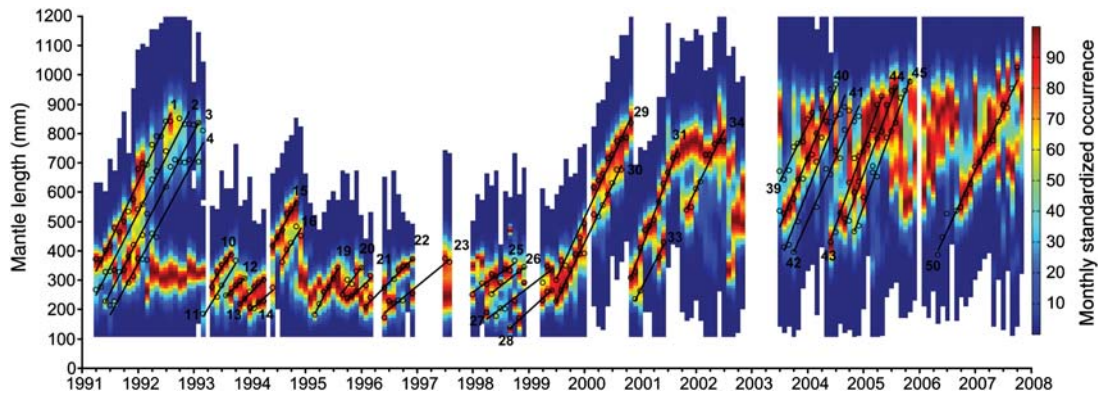
In four periods (represented by the numbered grey areas in Figure 6c), but for different reasons, no cohorts could be identified with certainty. During periods 1 and 2, the final ML of cohorts was just above the minimum size vulnerable to fisheries. For each of these cohorts, only the largest modes were available so no regression can be provided, i.e. the number of cohorts was identifiable but not the specific growth parameters (Figure 5). Nevertheless, in both periods, the stable MLs of the available modes indicate continuous spawning activity and sequences of new cohorts. For period 3 (2002/2003), no data were available and, although several cohorts are recognizable, these could not be determined definitively. During period 4 in the years 2004/2005, the existence of too many modes made specific cohorts indistinguishable. Discontinuous numbering of the cohorts identified indicates the possible number of cohorts that could not be identified clearly.

### Biological and environmental variability

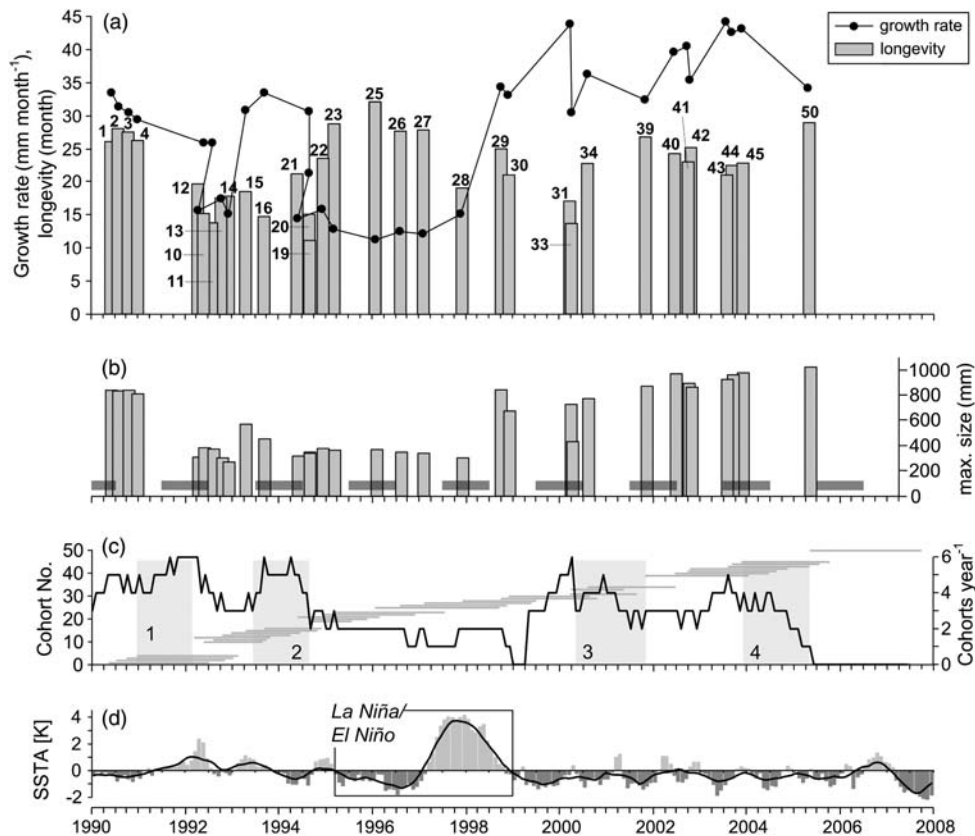
The linearly back-calculated hatching dates of the cohorts reveal that spawning was not restricted to the austral spring/summer, but took place throughout the year (Figure 7, Table 2). Although the season with the most number of cohorts is spring, autumn and winter see only slightly less spawning activity.



**Figure 4.** (a) Relationship between the VBGF and the assumed quasi-linear growth function of paedomorphic species; (b) the resulting growth function for three main life stages of *D. gigas*, with exponential growth of paralarvae/juveniles and a reduction in the growth rate attributable to the formation of reproductive tissue before death (min. size is size-at-first-capture in the Peruvian jumbo squid fishery). Maturity stages after Tafur and Rabí (1997).



**Figure 5.** Cohorts identified by LFA and the mean linkage with underlying monthly length frequencies recalculated from Gaussian modes identified. Open circles, maxima of the modes identified in the LFA; lines, regression fit to the modes of one cohort. The discontinuous numbering of cohorts indicates the existence of supposed missing cohorts that were not identified clearly.



**Figure 6.** Growth parameters of the cohorts identified and shown in Figure 5; (a) growth rates (line and dots) and longevity (bars), with the back-calculated time of hatching of each cohort given by the location of the points and the bars on the time axis; (b) the centres of the largest modes belonging to single cohorts, i.e. the mean size of the largest cohort of those identified, with horizontal bars representing austral spring/summer (October–March); (c) a plot of the temporal sequence of the cohorts identified in the study area (grey lines) and the number of cohorts entering the system in the following 12 months (line), with grey boxes indicating periods with presumably missing cohorts owing to the scarcity of identified modes (periods 1 and 2), missing data (period 3) and too many modes preventing clear identification and assignment to specific cohorts (period 4); (d) SST anomalies (SSTA) of the monitoring area EN 1 + 2 (Figure 1).

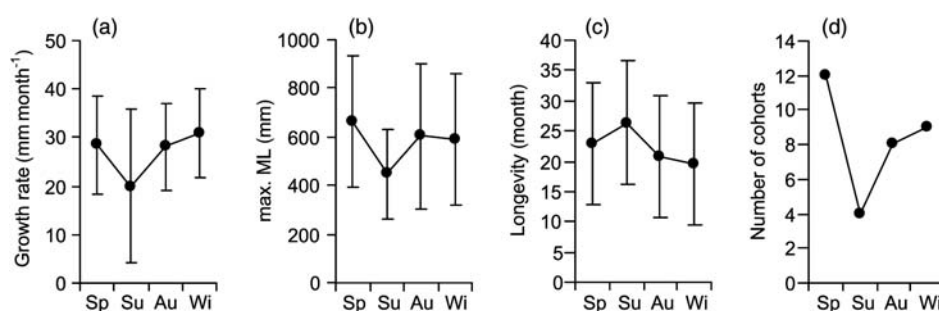
Summer is the only season with fewer cohorts identified, concurrent with the results of *Tafur et al. (2010)* that determined spawning activity from the ratio of mature females in the population and found a continuous increase in maturity after summer. Seasonal averages in the mean growth rates of cohorts, their maximum

size, and their longevity are not significantly different, although the mean growth rate and the mean maximum size of summer-hatched cohorts are lower than those of the other seasons. A tendency for a shorter lifespan for cohorts hatched during cooler months is clear. The characteristics of summer-hatched cohorts

**Table 2.** Growth parameters and back-calculated hatching date of the cohorts identified, with discontinuous numbering of cohorts indicating supposed missing cohorts that were not clearly identified.

Cohort	Maximum size (mm)	Growth rate (mm month <sup>-1</sup> )	Age (months)	Hatching date	Hatching season
1	841	33	25.9	1990.42	3
2	832	31	28.0	1990.58	4
3	836	31	27.5	1990.79	1
4	809	29	26.2	1990.99	1
10	386	26	15.2	1992.40	3
11	365	26	13.8	1992.60	4
12	304	16	19.6	1992.28	3
13	299	17	17.6	1992.79	1
14	273	15	17.8	1992.93	1
15	562	31	18.5	1993.29	3
16	450	33	14.7	1993.69	4
19	341	31	11.1	1994.66	4
20	342	21	15.1	1994.66	4
21	314	14	21.1	1994.41	3
22	372	16	23.6	1994.95	1
23	361	13	28.6	1995.20	2
25	366	11	32.1	1996.08	2
26	345	12	27.6	1996.61	4
27	335	12	27.8	1997.10	2
28	300	15	19.0	1997.92	1
29	836	34	24.9	1998.76	1
30	675	33	20.9	1998.92	1
31	728	44	17.1	2000.24	2
33	425	31	13.7	2000.28	3
34	773	36	22.7	2000.61	4
39	870	32	26.7	2001.86	1
40	967	40	24.2	2002.48	3
41	889	41	22.9	2002.76	1
42	858	35	25.2	2002.82	1
43	925	44	21.0	2003.59	4
44	957	43	22.5	2003.71	4
45	976	43	22.8	2003.93	1
50	1 024	34	28.8	2005.35	3
Mean	604.1	28	21.9		
s.d.	266.7	11	5.3		

Hatching date is shown in decimal form. Hatching seasons: 1, spring; 2, summer; 3, autumn; 4, winter (note that these are austral seasons).



**Figure 7.** Seasonal means and standard deviations of (a) growth rate, (b) largest mode, and (c) longevity; (d) the number of cohorts considered each season (Sp, spring; Su, summer; Au, autumn; Wi, winter) for statistical analysis.

with slow mean rates of growth, small terminal size, and extended longevity are similar to those of cohorts hatched during warm periods such as, for example, EN, indicating similar environmental conditions in summer and during warm periods.

The number of cohorts recruiting to fisheries per year is not constant (the line in Figure 6c), and again three periods can be identified. The number of new cohorts was between 0 and 6, and the overall mean number of new cohorts per year was 3.18

( $\pm 1.41$ ). During the early 1990s, an average of 4–5 cohorts entered the fishery in the subsequent 12 months after hatching. In the second period from 1995 to 1998, this number dropped to two, but rose again to three in the third period. In 1992, during period 1, there was a brief reduction to three annual cohorts. Cohorts identified without being able to obtain their growth parameters (not represented in Figure 6a) were used in addition for this analysis.

The slow growth rates of cohorts and small maximum sizes were derived for the 1992/1993 EN and the LN/EN event of 1996–1998. These events introduced great physical variability to the Peruvian HCS, as indicated by the anomalies in sea surface temperature (SST) of the EN 1 + 2 area shown in Figure 6d. The lag between biological response and physical environment that seems to exist is an artefact of the figure, because the cohorts in Figure 6a in the x-direction are placed at their respective hatching dates, i.e. the impact of environmental variation during their lives is ahead of them. This situation can be observed in Figure 6c, where the cohorts with the slowest growth rates (cohorts 12–14 and 21–28) are located exactly in the LN/EN period. However, none of mean growth rate, longevity, or maximum cohort size shows significant relationships with SST anomalies of the EN 1 + 2 area.

## Discussion

### Intra-annual vs. interannual variability

Growth and size-at-age depend on temperature and food availability in general (Atkinson and Sibly, 1997) and in cephalopods (Mangold, 1987). Intra-annual variability in the growth parameters of coleoid cephalopods with respect to the seasonal temperature change is a generally accepted phenomenon (Pauly, 1985; Forsythe and Van Heukelem, 1987; Pierce *et al.*, 1994; Hatfield, 2000; Villanueva, 2000; Wood and O'Dor, 2000; Semmens *et al.*, 2004). However, studies on interannual variability in growth parameters are scarce, perhaps because the period covered by available data in many studies is too short to evaluate such variability. Interannual variability in environmental conditions over short periods can often be less marked than intra-annual variability.

Interannual variability in the size-at-age of cohorts as a result of differences between cool and warm season temperatures was suggested for *Loligo gahi* by Hatfield (2000). For the Tasmanian *Sepioteuthis australis*, interannual variability in growth parameters and other life-history traits were described by Pecl *et al.* (2004). Growth and size of *Loligo vulgaris* varied in response to geographic differences in environmental conditions (Moreno *et al.*, 2002). Other research on interannual variability in growth parameters and longevity is limited and has been considered relatively unimportant compared with seasonal variability (Arkhipkin and Laptikhovsky, 1994; Nevárez-Martínez *et al.*, 2006). In contrast, our results show that for *D. gigas*, interannual variation in the mean growth rate is marked compared with intra-annual variation which, although noticeable, is not so obvious.

It was not possible to establish a significant linear relationship between SST anomalies in the EN 1 + 2 area and estimated growth parameters of *D. gigas*. The slow growth associated with cool (LN) and warm (EN) environmental conditions suggests a mixed source for variability in the growth parameters. It is assumed that slow growth rates during LN driven by the physiology of the animals could be a consequence of lower environmental temperatures. During the paralarval phase specifically, individual development of cephalopods is influenced by temperature (Lipiński, 2002). In this sense, growth rates during warm EN events could be expected to be higher than during cool or moderate periods, in contrast to the results here. However, growth processes are influenced not only by temperature but also by the availability of food (Mangold, 1987; Lipiński, 2002; Miyahara *et al.*, 2006). During

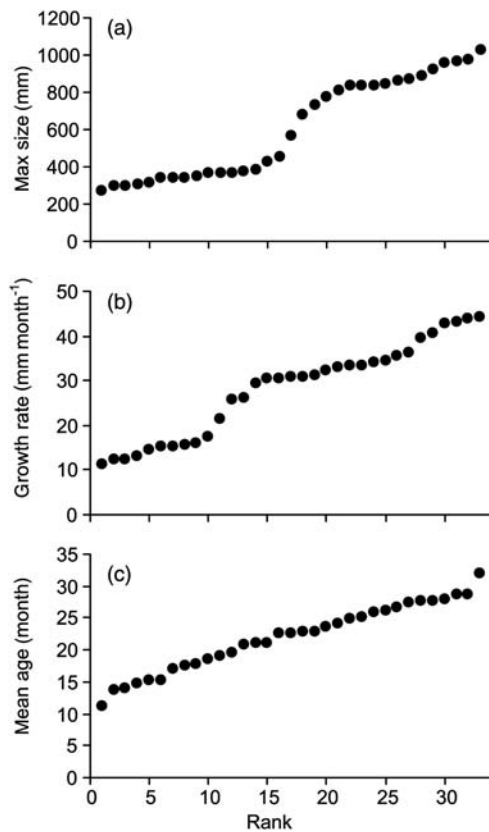
EN, the pelagic trophic system of the HCS changes to one that is less productive (Ayón *et al.*, 2008a, b). Therefore, it is assumed that the slow growth identified for cohorts during EN have an indirect ecological cause related to the quantity of food available to jumbo squid. Cohorts attained large maximum size mainly after the 1997/1998 EN, when the northern HCS has had moderately cool conditions (Figure 6d).

Large maximum size was attained only by the cohorts that also showed fast growth rates. This supports the proposal of Mangold (1987) that the onset of maturity is delayed when food is plentiful. The onset of maturity again governs the maximum size of an individual of a monocyclic species such as *D. gigas* and of cephalopods in general. The cohorts that completed their life cycle during the LN/EN period showed very slow growth. Their longevity was greater than that of the cohorts attaining the largest size, but their maximum size was among the smallest. This must lead to different size-at-age and consequently to implications for assessment and management.

The difference in growth parameters between cohort 21 and cohorts 19 and 20 (a difference that is less pronounced between cohort 12 and cohorts 10 and 11) that have nearly the same maximum size is of note and suggests the influence of another factor not covered by the analysis herein. Cohort 21 became much older than the two preceding cohorts (21.1 vs. 15.1 and 11.1 months; see Table 2) and their respective mean growth rates explain this change in longevity. However, the back-calculated dates of hatching reveal that all three cohorts hatched within less than 2 months. According to its growth parameters, cohort 21 was an LN/EN cohort that hatched even before cohorts 19 and 20, which are assumed to belong to the pre-LN/EN period (Figure 6). This may be the result of a limited spatial distribution of at least some cohorts in the Peruvian EEZ that makes it possible for fast-growing cohorts to remain in pre-LN/EN conditions, whereas slow-growing cohorts are already in conditions that the subsequent cohorts experience for some years thereafter. The development of EN events and the resulting spatial expansion of warmer water masses in the northern HCS are not instantaneous. They usually propagate along the coast from north to south over a period of several months, according to the strength of the event (Bertrand *et al.*, 2008), i.e. the northern part of the HCS and its biota may experience EN conditions whereas the central and the southern parts do not. To clarify the origin of the variation in growth-related parameters of coexisting cohorts, a spatially explicit analysis will be necessary in future. After all, the ability of a series of SST anomalies to reproduce large-scale distributions in environmental conditions is limited. Such one-dimensional data integrate the observed values of SST in an area, but cannot give information on the basis for those values, i.e. in the present case, which water masses contribute to the observations and to what extent. It is assumed that this would explain also why no clear correlation between growth parameters and SST anomalies was found.

Previously, the number of annual cohorts of *D. gigas* in the Gulf of California was reported to lie between one (Morales-Bojórquez, 2002) and five (Ehrhardt *et al.*, 1983). Here, the number of new cohorts recruiting to fisheries in the subsequent 12 months calculated for each month (Figure 6c) varied between zero and six. The period with the fewest entering cohorts was 1995–1998, corresponding to the LN/EN event, which we take as indication that spawning of jumbo squid depends on environmental conditions.





**Figure 8.** Ranked growth parameters of all the cohorts identified (Table 2); (a) maximum cohort size; (b) mean growth rate of cohort; (c) mean age.

### Size-at-maturity groups

When the maximum sizes of the cohorts identified are ranked, a continuous increase in maximum size becomes apparent, with a steep, step-like increase from around 450 to 800 mm between cohorts reaching small and large maximum sizes (Figure 8a). As maximum size and size-at-maturity are related through the monocyclic spawning pattern of *D. gigas* (Rocha *et al.*, 2001; Tafur *et al.*, 2010), the existence of three groups of size-at-maturity as proposed earlier (Nesis, 1983; Nigmatullin *et al.*, 2001) is doubtful, at least in this study area. The restriction of the different groups of size-at-maturity to specific parts of the distribution of jumbo squid is not supported by the results of this study in the Peruvian EEZ, which are interpreted as there being two major groups of size-at-maturity, coinciding with the doubts about the existence of three groups expressed by Nesis (1970). A similar continuous transition between size extremes was proposed by Tafur *et al.* (2010), who calculated the seasonal values of size-at-maturity and an individual maturity index for jumbo squid in the Peruvian EEZ. Two other explanations are possible: (i) further cohorts in the range 450–600 mm are missing owing to the incomplete coverage of existing sizes, or (ii) jumbo squid response to changing environmental conditions is a combination of variations in the maximum size along with changes in the cohort growth rate and longevity. However, these parameters do not show the same trajectory when ranked (Figure 8b and c), and instead either point to the existence of three groups (cohort growth rates) or no grouping at all (longevity). Although it is not possible to conclude the source

of the variability of the growth parameters, the differences in the transitions of growth parameters observed do seem to support phenotypic plasticity as the origin.

### Discrepancy between statolith analysis and MPA

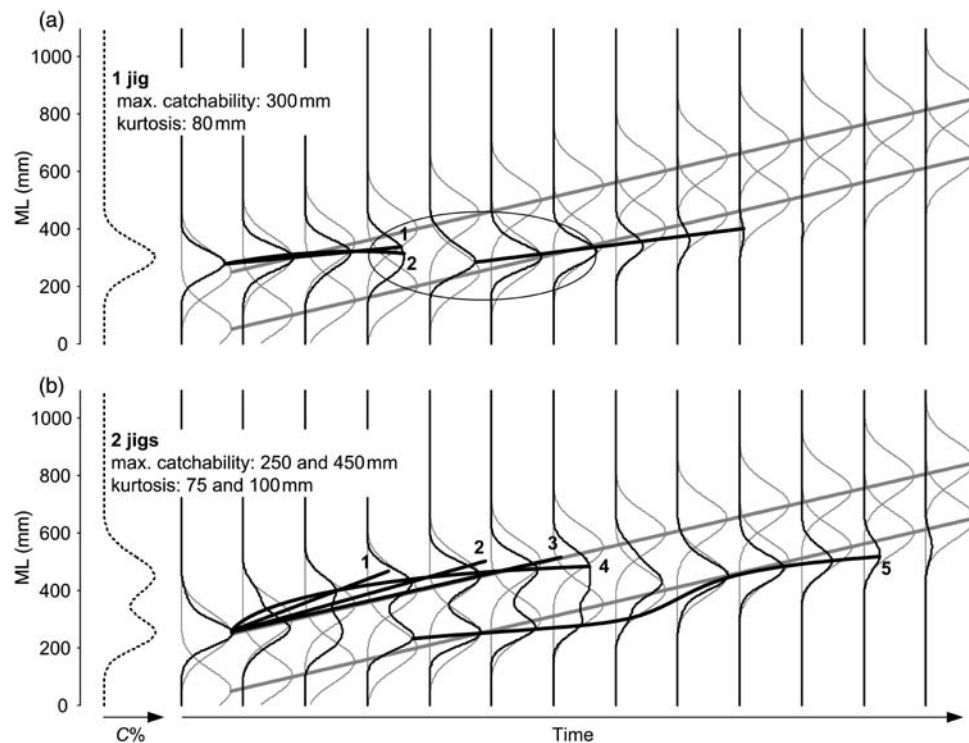
Discrepancy between the results obtained from otolith/statolith analysis and MPA is common (Ralston and Williams, 1988; Morales-Nin, 1989a, b; Hammers and Miranda, 1991; Arkhipkin *et al.*, 2000; references in Jackson *et al.*, 2000) and has also been found for *D. gigas* (Table 1). The results of the present study identify a number of cohorts from 1991 to 1994 and longevities of 1–2 years, supporting the results obtained by Argüelles (1996) using MPA. However, the results are not consistent with the statolith analysis of Argüelles *et al.* (2001) that determined maximal longevities of <1 year for jumbo squid in the same period. Similar dichotomy was found for the 2002 cohorts that here were found to live for up to 2 years, whereas the statolith analysis for squid hatched the same year suggested a lifespan of a maximum of 1 year (C. Goicochea, IMARPE, unpublished data). Greater divergence still was observed for the cohorts of 1997 and 1998, for which the present study found a longevity of 19–32 months whereas a statolith analysis found <200 rings in mature animals ( $n = 20$ ) of the same period and size (JA, unpublished data). In general, the results obtained from all statolith analyses of *D. gigas* match each other, as do the current results with other results using MPA (Table 1). The limitations of both methods therefore need to be discussed further in an attempt to shed light on the possible reasons for the disagreement.

For the MPA, a number of caveats were advanced that led to the rejection of its use in growth estimation of squid in the 1990s (Caddy, 1991; Pierce *et al.*, 1994; Jackson *et al.*, 2000). Migration (Hatfield and Rodhouse, 1994), the existence of microcohorts that cannot be distinguished (Caddy, 1991), and the use of erroneous growth functions through incorrect temporal resolution or inadequate spatial pooling of length frequency data have all been assumed to result in skewed growth rates and longevity (Pierce *et al.*, 1994; Jackson *et al.*, 2000). For the present study, the conventional form of MPA (e.g. ELEFAN) was amplified in several points to overcome some of its known limitations.

No study has been published on the migration of *D. gigas* in the southern hemisphere, so it remains unknown whether the species has a migration pattern similar to that of other ommastrephids. In this work, the problem of a bias introduced by migration was addressed by pooling the data from a large area that supposedly included most of the large-scale movement patterns that might take place. The monthly resolution of length frequency data used in the MPA is also justified considering the longevity of 1–4 years proposed by other workers (Table 1) and also found in this analysis. The linear middle portion of a tripartite growth function (Figure 4b) was used to calculate the growth parameters of the cohorts identified, and the results agree with those derived from the quasi-linear growth form found in the statolith analysis of *D. gigas* (Argüelles *et al.*, 2001) and the statolith analysis of other cephalopods (Masuda *et al.*, 1998; Rodhouse, 1998; Hatfield, 2000; Yatsu, 2000).

Another factor that leads to underestimation of growth rates in a MPA and that to our knowledge has not been taken into account in this context is the two-sided size selectivity of the jigs. It introduces an observation bias leading to skewed modes in the length frequency data (see the length frequency distribution decomposition model and Figure 3). Jigs are used to fish jumbo





**Figure 9.** Two hypothetical cohorts with linear growth through 13 time-increments (grey-lined modes), with observation bias in growth caused by the fishing gear (here, jigs) having different size-dependent catchabilities ( $C\%$ ; broken black lines), and the resulting growth functions (real, grey lines; observed, black lines); (a) observation with one jig size resulting in underestimation of growth rate and an unclear growth function; (b) observation with two jig sizes showing potentially incorrect growth rates and functions; the x-axis of each time-increment is the frequency of occurrence per size class, and the numbers of observed growth functions indicate different types of possible growth function.

squid and many other squid species (Rathjen, 1991). To be effective, this fishing gear must be adjusted constantly to the size range of target squid present in the water, and many sizes of jigs are in use. The results of a preliminary study with four jig sizes (described as small, medium, large, and extra large) deployed on at least three cohorts present in the water at the same time reveal a Gaussian function for selectivity, with maximum catchability at 300, 310, 540, and 830 mm for the four jig sizes used (JA, unpublished data). To understand the effects of biased observation on the MPA, two subsequent hypothetical cohorts with linear growth were compared with the results obtained from size-selective observation of jig performance on these cohorts (Figure 9). The examples show that selectivity can result in erroneous growth rates and even in incorrect growth functions. To prevent such incorrect results when using the MPA, it is necessary that the gear deployed covers most of the size range of the target species. If this is not the case, as was the situation here, a correction for observation bias is needed.

Observation bias is introduced because of missing, delayed, or incomplete adjustment of jig size to target size. The present study corrected for such bias. The large number of cohorts per year found for *D. gigas* (Figure 6c) results in the continuous entry of new cohorts that are underestimated when observed (i.e. fished) with specific jig sizes and without correction for observation bias. Analysis of the monthly length frequency in 60% of the 175 months used the length frequency model with observation bias adjustment (i.e. the Gaussian observation function) to

correct the observed modes to supposedly real values. The parameters obtained for the jig functions are variable, even from one month to the next, so reproducing the high variability in jig types employed in the fishery. The variable use of jig sizes seems logical: to optimize economic benefit, jig size (i.e. size selectivity) needs to be adjusted to the ML of the cohorts present during the fishing operation. Although no hard data are available on this topic, information on rapid changing of jigs is supported by anecdotal reports of on-board technical observers. However, fishing by adjusting the gear to the size range of the most abundant cohort or cohorts will always imply that other, less abundant cohorts whose size range is smaller or bigger than the size being targeted will be underrepresented in the catch. Whenever the number of jig sizes is less than the number of cohorts in the water, the observation is biased and needs to be corrected to obtain the real length frequency.

With few exceptions (Pierce *et al.*, 1994; Hatfield, 2000, and the seasonally oscillating VBGF), variable growth rates have not been used in evaluating the growth parameters of cephalopod populations. The present results suggest that intercohort (i.e. interannual) variability in growth parameters is an unavoidable effect related to changed environmental conditions that needs to be considered in estimating growth parameters. MPA usually cannot include variability in growth parameters. The phenotypic plasticity of cephalopods is widely accepted as one of their main characteristics (Boyle and Boletzky, 1996), so it is unsurprising that previous investigations on cephalopod growth using the MPA

would contribute to the belief that the method is not suitable for cephalopods (Semmens *et al.*, 2004).

The estimated growth parameters of the present study are similar to those of the MPA of Argüelles (1996) for 1991 cohorts but not consistent with those derived from statolith analysis of the same cohorts carried out by Argüelles *et al.* (2001). Growth rates of 383 mm year<sup>-1</sup> (range 365–547 mm year<sup>-1</sup>) were determined from a tag-recapture study of *D. gigas* in the Gulf of California in 2001/2002 (Markaida *et al.*, 2005), values similar to the 336 mm year<sup>-1</sup> ( $\pm 132$  mm year<sup>-1</sup>) found here for the Peruvian population. Methodological improvements put in place for the present study and the similarity of the results with those of tag-recapture for another stock may therefore be indicative of shortcomings in statolith analysis for *D. gigas*. Possible sources of bias in that method are discussed below.

A major concern with statolith analysis is the fact that for many cephalopods, including *D. gigas*, the assumed daily formation of statolith rings has not been confirmed. Verification of daily formation of statolith rings has been conducted by relative few workers on laboratory-reared animals and in some field experiments (e.g. Lipiński *et al.*, 1998). Long-term rearing of jumbo squid has not been successful to date (W. Gilly, Hopkins Marine Station, pers. comm.), so direct validation of the one-mark-per-day assumption will be difficult.

Statoliths in many respects are similar to the better studied otoliths of teleosts. Their rings are dark, proteinaceous areas formed in response to feeding activity that often has a regular diel basis (Radtke, 1983). Factors such as temperature (Durholtz and Lipiński, 2000; Villanueva, 2000; Chung and Lu, 2005; Zumholz *et al.*, 2007a), age (Bettencourt and Guerra, 2000, 2001), body size (Hüssy, 2008a), activity level, oxygen availability, pH (Morris, 1991), and feeding level (Spratt, 1979; Zumholz *et al.*, 2006; Hüssy, 2008b) are all known to influence the accretion process of otoliths/statoliths and their legibility. Additionally, the statoliths of paralarvae do show indistinct increments (Yatsu *et al.*, 1999).

Oxygen limitation leads to blurred areas without rings towards the margins of the statoliths of older squid, so making it possible to underestimate the real age of squid (Pauly, 1998). One of the outstanding features of jumbo squid is their remarkable tolerance of hypoxia, which not only allows them to inhabit the prominent oxygen minimum layer (OML) of the eastern Pacific perhaps as a shelter from predators, as do small pelagic fish, but also to move and hunt actively for hours under hypoxic conditions (Gilly *et al.*, 2006; Zeidberg and Robison, 2007; Rosa and Seibel, 2008). Knowing that oxygen levels do influence the formation of otoliths (Sepúlveda, 1994) and statoliths (Morris, 1991; Lipiński, 1993; Pauly, 1998), we assume that frequent visits by jumbo squid to the OML (Gilly *et al.*, 2006; Bazzino *et al.*, 2010) can certainly affect the formation and readability of their statoliths, i.e. that such behaviour may result in missing statolith rings in bleached areas (*sensu* Pauly, 1998). The consequence would be a serious underestimation of the real age and overestimation of the growth rate of jumbo squid determined from statolith analysis.

Verification of the one-mark-per-day hypothesis itself may have limitations because statolith formation is influenced by food availability (Spratt, 1979; Zumholz *et al.*, 2006). In laboratory experiments, regular feeding once or a few times per day is customary (Dawe *et al.*, 1985; Bettencourt and Guerra, 2001), likely restricted to working hours, and that could also lead to the production of regular daily growth increments. *Dosidicus gigas* apparently feeds in the OML by day (Zeidberg and Robison, 2007; Rosa

and Seibel, 2010) and near the surface at night (Nigmatullin *et al.*, 2001), so daily ring formation under a traditional laboratory feeding regime could be a rearing artefact that may be absent in the wild. Moreover, several studies (e.g. Durholtz and Lipiński, 2000; Villanueva, 2000; Chung and Lu, 2005) have noted the significant effect of temperature on the growth and mark deposition of statoliths. Chung and Lu (2005) offer an explanation how this may lead to underestimation of ring number: low temperature resulting in slow statolith growth and reduction of the distance between daily rings deposited to values below 1  $\mu$ m, which are assumed to be difficult to distinguish.

The MPA method used in this work has attempted to address some of the previously expressed criticism of the method, but more experimental work will have to be conducted to clarify further the real reasons for the dichotomy in the results of various growth determination methods and their respective plausibility. We suggest that the use of electronic tags (Gilly *et al.*, 2006) along with nanoscale chemical analysis using secondary ion mass spectrometry (NanoSIMS) of statoliths (Zumholz *et al.*, 2007b) may be able to advance understanding of cephalopod growth and the formation of the microincrements in their statoliths.

To conclude, the variability in growth parameters found here is assumed to be the result of a dependence on environmental conditions, although no direct link was traced to a single factor. It is assumed that a mixed impact of temperature and food availability control growth rates and the onset of maturation, which together define longevity and maximum size. The possibility of altering growth parameters allows *D. gigas* to react to changes in productivity and extreme temperature events. Under favourable environmental conditions, jumbo squid not only more than triple their size and growth rate, but also increase their frequency of spawning to use available energy optimally.

The results of this work on growth using MPA do not mirror the results of studies that investigate cephalopod growth by statolith analysis, but do agree with other MPA values and the results of the only tag-recapture study conducted thus far for *D. gigas*. For cephalopods it has been proposed not to rely on a single method of age determination (Caddy, 1991). Nevertheless, a MPA can be sufficient when using a tailored solution that allows for (i) multiple annual cohorts, (ii) the selection of an appropriate growth function, (iii) the incorporation of interannual variability in growth parameters, and (iv) a correction for observation bias introduced by restricted catchability as a function of size. MPA methods that cannot meet these requirements should, however, not be used or at least be revised very carefully with respect to their suitability for each specific case.

## Acknowledgements

We thank all our colleagues at IMARPE that supported our work with knowledge, experience, and advice, especially those from the Marine Invertebrate Department and all on-board observers. We thank M. Wolff for his willingness to develop ideas with us during elaboration of discussion, and the two anonymous reviewers for valued suggestions on improvement to the submitted manuscript. FK was financed in part by CENSOR.

## References

- Argüelles, J. 1996. Crecimiento y reclutamiento del calamar gigante *Dosidicus gigas* en el Perú (1991 a 1994). Informe Instituto del Mar del Perú, 23: 3–14.

- Argüelles, J., Rodhouse, P. G., Villegas, P., and Castillo, G. 2001. Age, growth and population structure of the jumbo flying squid *Dosidicus gigas* in Peruvian waters. *Fisheries Research*, 54: 51–61.
- Argüelles, J., Tafur, R., Taipe, A., Villegas, P., Keyl, F., Dominguez, N., and Salazar, M. 2008. Size increment of jumbo flying squid *Dosidicus gigas* mature females in Peruvian waters, 1989–2004. *Progress in Oceanography*, 79: 308–312.
- Arkhipkin, A., Jereb, P., and 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 Journal of Marine Science*, 57: 31–41.
- Arkhipkin, A., and Laptikhovsky, V. 1994. Seasonal and interannual variability in growth and maturation of winter-spawning *Illex argentinus* (Cephalopoda, Ommastrephidae) in the Southwest Atlantic. *Aquatic Living Resources*, 7: 221–232.
- Atkinson, D., and Sibly, R. M. 1997. Why are organisms usually bigger in colder environments? Making sense of a life history puzzle. *Trends in Ecology and Evolution*, 12: 235–239.
- Ayón, P., Criales-Hernandez, M. I., Schwaborn, R., and Hirche, H.-J. 2008a. Zooplankton research off Peru: a review. *Progress in Oceanography*, 79: 238–255.
- Ayón, P., Swartzman, G., Bertrand, A., Gutiérrez, M., and Bertrand, S. 2008b. Zooplankton and forage fish species off Peru: large-scale bottom-up forcing and local-scale depletion. *Progress in Oceanography*, 79: 208–214.
- Bazzino, G., Gilly, W. F., Markaida, U., Salinas-Zavala, C. A., and Ramos-Castillejos, J. 2010. Horizontal migrations, vertical habitat utilization and diet of the jumbo squid (*Dosidicus gigas*) in the Pacific Ocean off Baja California Sur, Mexico. *Progress in Oceanography*, 86: 59–71.
- Bazzino, G., Salinas-Zavala, C. A., and Markaida, U. 2007. Variability in the population structure of jumbo squid (*Dosidicus gigas*) in Santa Rosalia, central Gulf of California. *Ciencias Marinas*, 33: 173–186.
- Bertrand, S., Dewitte, B., Tam, J., Díaz, E., and Bertrand, A. 2008. Impacts of Kelvin wave forcing in the Peru Humboldt Current system: scenarios of spatial reorganizations from physics to fishers. *Progress in Oceanography*, 79: 278–289.
- Bettencourt, V., and Guerra, A. 2000. Growth increments and biomineralization process in cephalopod statoliths. *Journal of Experimental Marine Biology and Ecology*, 248: 191–205.
- Bettencourt, V., and Guerra, A. 2001. Age studies based on daily growth increments in statoliths and growth lamellae in cuttlebone of cultured *Sepia officinalis*. *Marine Biology*, 139: 327–334.
- Boyle, P. R., and Boletzky, S. v. 1996. Cephalopod populations: definitions and dynamics. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences*, 351: 985–1002.
- Caddy, J. F. 1991. Daily rings on squid statoliths: an opportunity to test standard population models? In *Squid Age Determination Using Statoliths*, pp. 53–66. Ed. by P. Jereb, S. Ragonese, and S. von Boletzky. Instituto di Tecnologia della Pesca e del Pescato (ITTP-CNR), Mazara del Vallo, Italy.
- Chung, W.-S., and Lu, C.-C. 2005. The influence of temperature and salinity on the statolith of the oval squid *Sepioteuthis lessoniana* Lesson, 1830 during early developmental stages. *Phuket Marine Biological Centre Research Bulletin*, 66: 175–185.
- Dawe, E. G., O'Dor, R. K., Odense, P. H., and Hurley, G. V. 1985. Validation and application of an ageing technique for short-finned squid (*Illex illecebrosus*). *Journal of Northwest Atlantic Fishery Science*, 6: 107–116.
- Day, T., and Taylor, P. D. 1997. Von Bertalanffy's growth equation should not be used to model age and size-at-maturity. *The American Naturalist*, 149: 381–393.
- Durholtz, M. D., and Lipiński, M. R. 2000. Influence of temperature on the microstructure of statoliths of the thumbstall squid *Lolliguncula brevis*. *Marine Biology*, 136: 1029–1037.
- Ehrhardt, N. M., Jacquemin, P. S., Garcia, B. F., Gonzales, D. G., Lopez, J. M., Ortiz, C. J., and Solis, N. A. 1983. Summary of the fishery and biology of the jumbo squid (*Dosidicus gigas*) in the Gulf of California, Mexico. *Memoirs of the National Museum of Victoria*, 44: 305–311.
- Field, J. C., Baltz, K., Phillips, A. J., and Walker, W. A. 2007. Range expansion and trophic interactions of the jumbo squid, *Dosidicus gigas*, in the California Current. *CalCOFI Reports*, 47: 131–146.
- Forsythe, J. W., and Van Heukelem, W. F. 1987. Growth. In *Cephalopod Life Cycles. 2. Comparative Reviews*, pp. 135–156. Ed. by P. R. Boyle. Academic Press, London.
- Gilly, W. F., Markaida, U., Baxter, C. H., Block, B. A., Boustany, A., Zeidberg, L., Reisenbichler, K., et al. 2006. Vertical and horizontal migrations by the jumbo squid *Dosidicus gigas* revealed by electronic tagging. *Marine Ecology Progress Series*, 324: 1–17.
- Hammers, B. E., and Miranda, L. E. 1991. Comparison of methods for estimating age, growth, and related population characteristics of white crappies. *North American Journal of Fisheries Management*, 11: 492–498.
- Hatanaka, H., Kawahara, S., Uozumi, Y., and Kasahara, S. 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 Scientific Council Studies*, 9: 59–68.
- Hatfield, E. M. C. 2000. Do some like it hot? Temperature as a possible determinant of variability in the growth of the Patagonian squid, *Loligo gahi* (Cephalopoda: Loliginidae). *Fisheries Research*, 47: 27–40.
- Hatfield, E. M. C., and Rodhouse, P. G. 1994. Migration as a source of bias in the measurement of cephalopod growth. *Antarctic Science*, 6: 179–184.
- Hüssy, K. 2008a. Otolith accretion rates: does size really matter? *Journal of Experimental Marine Biology and Ecology*, 362: 131–136.
- Hüssy, K. 2008b. Otolith shape in juvenile cod (*Gadus morhua*): ontogenetic and environmental effects. *Journal of Experimental Marine Biology and Ecology*, 364: 35–41.
- Jackson, G. D., Alford, R. A., and Choat, J. H. 2000. Can length frequency analysis be used to determine squid growth? An assessment of ELEFAN. *ICES Journal of Marine Science*, 57: 948–954.
- Keyl, F., Argüelles, J., Mariátegui, L., Tafur, R., Wolff, M., and Yamashiro, C. 2008. A hypothesis on range expansion and spatio-temporal shifts in size-at-maturity of jumbo squid (*Dosidicus gigas*) in the eastern Pacific Ocean. *CalCOFI Reports*, 49: 119–128.
- Lipiński, M. R. 1993. The deposition of statoliths: a working hypothesis. In *Recent Advances in Cephalopod Fisheries Biology*, pp. 241–262. Ed. by T. Okutani, R. K. O'Dor, and T. Kubodera. Tokai University Press, Tokyo.
- Lipiński, M. R. 2002. Growth of cephalopods: conceptual model. *Abhandlungen der Geologischen Bundesanstalt*, 57: 133–138.
- Lipiński, M. R., Durholtz, M. D., and Underhill, L. G. 1998. Field validation of age readings from the statoliths of chokka squid (*Loligo vulgaris reynaudii* d'Orbigny, 1845) and an assessment of associated errors. *ICES Journal of Marine Science*, 55: 240–257.
- Mangold, K. 1987. Reproduction. In *Cephalopod Life Cycles. 2. Comparative Reviews*, pp. 157–200. Ed. by P. R. Boyle. Academic Press, London.
- Markaida, U., Quiñónez-Velázquez, C., and Sosa-Nishizaki, O. 2004. Age, growth and maturation of jumbo squid *Dosidicus gigas* (Cephalopoda: Ommastrephidae) from the Gulf of California, Mexico. *Fisheries Research*, 66: 31–47.
- Markaida, U., Rosenthal, J. J. C., and Gilly, W. F. 2005. Tagging studies on the jumbo squid (*Dosidicus gigas*) in the Gulf of California, Mexico. *Fishery Bulletin US*, 103: 219–226.
- Masuda, S., Yokawa, K., Yatsu, A., and Kawahara, S. 1998. Growth and population structure of *Dosidicus gigas* in the southeastern Pacific Ocean. In *Contributed Papers to International*



- Symposium on Large Pelagic Squids, 18–19 July 1996, pp. 107–118. Ed. by T. Okutani. Japan Marine Fishery Resources Research Center, Tokyo.
- Mejia-Rebollo, A., Quiñónez-Velázquez, C., Salinas-Zavala, C. A., and Markaida, U. 2008. Age, growth and maturity of jumbo squid (*Dosidicus gigas* d'Orbigny, 1835) off the western coast of the Baja California peninsula. *CalCOFI Reports*, 49: 256–262.
- Miyahara, K., Ota, T., Goto, T., and Gorie, S. 2006. Age, growth and hatching season of the diamond squid *Thysanoteuthis rhombus* estimated from statolith analysis and catch data in the western Sea of Japan. *Fisheries Research*, 80: 211–220.
- Morales-Bojórquez, E. 2002. Comments about the relationship between temperature and giant squid catches. *Ciencias Marinas*, 28: 211–221.
- Morales-Nin, B. 1989a. Age and growth of the southern stock of Peruvian anchoveta based on otolith microstructures and length-frequency analysis. In *The Peruvian Upwelling Ecosystem: Dynamics and Interactions*, pp. 179–188. Ed. by D. Pauly, P. Muck, J. Mendo, and I. Tsukayama. Instituto del Mar del Perú (IMARPE), Callao, Perú.
- Morales-Nin, B. 1989b. Growth determination of tropical marine fishes by means of otolith interpretation and length frequency analysis. *Aquatic Living Resources*, 2: 241–253.
- Moreno, A., Pereira, J., Arvanitidis, C., Robin, J.-P., Koutsoubos, D., Perales-Raya, C., Cunha, M. M., et al. 2002. Biological variation of *Loligo vulgaris* (Cephalopoda: Loliginidae) in the eastern Atlantic and Mediterranean. *Bulletin of Marine Science*, 71: 515–534.
- Morris, C. C. 1991. Statocyst fluid composition and its effects on calcium carbonate precipitation in the squid *Alloteuthis subulata* (Lamarck, 1798): towards a model for biomineralization. *Bulletin of Marine Science*, 49: 379–388.
- Nesis, K. N. 1970. The biology of the giant squid of Peru and Chile, *Dosidicus gigas*. *Oceanology*, 10: 108–118.
- Nesis, K. N. 1983. *Dosidicus gigas*. In *Cephalopod Life Cycles. 1. Species Accounts*, pp. 215–231. Ed. by P. R. Boyle. Academic Press, London.
- Nevárez-Martínez, M. O., Méndez-Tenorio, F. J., Cervantes-Valle, C., López-Martínez, J., and Anguiano-Carrasco, M. L. 2006. Growth, mortality, recruitment, and yield of the jumbo squid (*Dosidicus gigas*) off Guaymas, Mexico. *Fisheries Research*, 79: 38–47.
- Nigmatullin, C. M., Arkhipkin, A. I., and Sabirov, R. M. 1995. Age, growth and reproductive biology of diamond-shaped squid *Thysanoteuthis rhombus* (Oegopsida: Thysanoteuthidae). *Marine Ecology Progress Series*, 124: 73–87.
- Nigmatullin, C. M., Nesis, K. N., and Arkhipkin, A. I. 2001. A review of the biology of the jumbo squid *Dosidicus gigas* (Cephalopoda: Ommastrephidae). *Fisheries Research*, 54: 9–19.
- Pauly, D. 1985. Population dynamics of short lived species with emphasis on squids. *NAFO Scientific Council Studies*, 9: 143–154.
- Pauly, D. 1998. Why squid, though not fish, may be better understood by pretending they are. *South African Journal of Marine Science*, 20: 47–58.
- Pecl, G. T., Moltschaniwskyj, N. A., Tracey, S. R., and Jordan, A. R. 2004. Inter-annual plasticity of squid life history and population structure: ecological and management implications. *Oecologia*, 139: 515–524.
- Pierce, G. J., Boyle, P. R., Hastie, L. C., and Key, L. 1994. The life history of *Loligo forbesi* (Cephalopoda: Loliginidae) in Scottish waters. *Fisheries Research*, 21: 17–41.
- Radtko, R. L. 1983. Chemical and structural characteristics of statoliths from the short-finned squid *Illex illecebrosus*. *Marine Biology*, 76: 47–54.
- Ralston, S. V., and Williams, H. A. 1988. Depth distributions, growth and mortality of deep slope fishes from the Mariana Archipelago. NOAA Technical Memorandum, NMFS 113. 47 pp.
- Rathjen, W. F. 1991. Cephalopod capture methods: an overview. *Bulletin of Marine Science*, 49: 494–505.
- Rocha, F., Guerra, Á., and Gonzalez, Á. F. 2001. A review of reproductive strategies in cephalopods. *Biological Review*, 76: 291–304.
- Rodhouse, P. G. 1998. Physiological progenesis in cephalopod molluscs. *Biological Bulletin*, 195: 17–20.
- Rosa, R., and Seibel, B. A. 2008. Synergistic effects of climate-related variables suggest future physiological impairment in a top oceanic predator. *Proceedings of the National Academy of Sciences of the USA*, 105: 20776–20780.
- Rosa, R., and Seibel, B. A. 2010. Metabolic physiology of the Humboldt squid, *Dosidicus gigas*: implications for vertical migration in a pronounced oxygen minimum zone. *Progress in Oceanography*, 86: 72–80.
- Rosas-Luis, R., Salinas-Zavala, C. A., Koch, V., Del Monte Luna, P., and Morales-Zárate, M. V. 2008. Importance of jumbo squid *Dosidicus gigas* (Orbigny, 1835) in the pelagic ecosystem of the central Gulf of California. *Ecological Modelling*, 218: 149–161.
- Semmens, J. M., Pecl, G. T., Villanueva, R., Jouffre, D., Sobrino, I., Wood, J. B., and Rigby, P. R. 2004. Understanding octopus growth: patterns, variability and physiology. *Marine and Freshwater Research*, 55: 367–377.
- Sepúlveda, A. O. 1994. Daily growth increments in the otoliths of European smelt *Osmerus eperlanus* larvae. *Marine Ecology Progress Series*, 108: 33–42.
- Spratt, J. D. 1979. Age and growth of the market squid, *Loligo opalescens* Berry, from statoliths. *CalCOFI Reports*, 20: 58–64.
- Swartzman, G., Bertrand, A., Gutiérrez, M., Bertrand, S., and Vasquez, L. 2008. The relationship of anchovy and sardine to water masses in the Peruvian Humboldt Current System from 1983 to 2005. *Progress in Oceanography*, 79: 228–237.
- Tafur, R., Keyl, F., and Argüelles, J. 2010. Reproductive biology of the jumbo squid (*Dosidicus gigas*) as related to size and environmental variability in the northern Humboldt Current system. *Marine Ecology Progress Series*, 400: 127–141.
- Tafur, R., and Rabí, M. 1997. Reproduction of the jumbo flying squid, *Dosidicus gigas* (Orbigny, 1835) (Cephalopoda: Ommastrephidae) off Peruvian coasts. *Scientia Marina*, 61 (Suppl. 2): 33–37.
- Villanueva, R. 2000. Effect of temperature on statolith growth of the European squid *Loligo vulgaris* during early life. *Marine Biology*, 136: 449–460.
- Wood, J. B., and O'Dor, R. K. 2000. Do larger cephalopods live longer? Effects of temperature and phylogeny on interspecific comparisons of age and size at maturity. *Marine Biology*, 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 Agriculture Research Quarterly*, 34: 75–80.
- Yatsu, A., Tafur, R., and Maravi, C. 1999. Embryos and rhynchoteutian paralarvae of the jumbo flying squid *Dosidicus gigas* (Cephalopoda) obtained through artificial fertilization from Peruvian waters. *Fisheries Science*, 65: 904–908.
- Zeidberg, L. D., and Robison, B. H. 2007. Invasive range expansion by the Humboldt squid, *Dosidicus gigas*, in the eastern North Pacific. *Proceedings of the National Academy of Sciences of the USA*, 104: 12948–12950.
- Zumholz, K., Hansteen, T., Hillion, F., Horreard, F., and Piatkowski, U. 2007b. Elemental distribution in cephalopod statoliths: NanoSIMS provides new insights into nano-scale structure. *Reviews in Fish Biology and Fisheries*, 17: 487–491.
- Zumholz, K., Hansteen, T., Klügel, A., and Piatkowski, U. 2006. Food effects on statolith composition of the common cuttlefish (*Sepia officinalis*). *Marine Biology*, 150: 237–244.
- Zumholz, K., Hansteen, T. H., Piatkowski, U., and Croot, P. L. 2007a. Influence of temperature and salinity on the trace element incorporation into statoliths of the common cuttlefish (*Sepia officinalis*). *Marine Biology*, 151: 1321–1330.