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Spatial and temporal variation in age and growth in juvenile *Loligo forbesi* and relationships with recruitment in the English Channel and Scottish waters

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Abstract

In many cephalopod stocks, resource abundance and fishing yields depend on the recruitment of the annual cohort. Loliginid squids such as *Loligo forbesi* are present in the English Channel and in Scottish waters. Variation in age and growth in juvenile *Loligo forbesi* of these two areas was investigated at the spatial and temporal scale, and inter-annual differences in growth were related to recruitment variation to test density dependence in squid growth in both populations. Spatial and temporal differences in growth were analysed in five cohorts that showed marked differences in recruitment abundance. Biological sampling showed that recruitment occurred in late autumn and spring in Scottish waters and in summer in the English Channel. In both fishing seasons, monthly samples collected at fish markets were analysed and ages of juveniles (mantle length <200 mm) were determined using daily statolith growth increments. Age determination indicated that recruits were older than previously thought (about 8 to 11 months). Back-calculated hatching dates were used to estimate growth variation during the pre-recruitment stage. Exponential growth models adequately described size-at-age data. Linear modelling demonstrated inter-annual and spatial significant differences in growth rates. Influence of the hatching month (within or between cohorts) on growth was detected. To improve our understanding of recruitment variability, this study addresses the question: Does early growth vary in relation with recruitment? Available recruitment estimates appeared to be related to annual growth rates; density dependence in squid growth is suggested for the English Channel population.

Keywords: Age; Exponential growth; Squid; Statoliths; Recruitment; Density dependence

1. Introduction

Loligo forbesi is a loliginid squid, ranging from 20°S on the west coast of Africa to 63°N in the north-east Atlantic (Roper et al., 1984). This is the most abundant squid species caught by fishermen in the northern northeast Atlantic (Boyle and Pierce, 1994; Pierce et al., 1994b; Robin and Boucaud-Camou, 1995). As in most cephalopod fisheries, substantial inter-annual differences in catches have occurred in recent years (Pierce et al., 1998; Pierce and Boyle, 2003; Royer et al., 2002; Young et al., 2004). Because cephalopods are short-lived and generations usually do not overlap, stock dynamics depend entirely on recruit-

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ment success. In fisheries management, recruitment is defined as the renewal of smaller size classes in a stock. Recruitment is a complex process that extends over several months, probably because of extended hatching. In Scottish waters, major peaks in recruitment occur in April and November (Collins et al., 1997, 1999), but some recruits appear in the fishery throughout the year (Lum-Kong et al., 1992). In the English Channel, recruitment happens mainly during the summer (Holme, 1974), although Holme (1974) also recognised the presence of a summer breeding population. High inter-annual fluctuations in recruitment are observed in both areas (Royer et al., 2002; Young et al., 2004). Why is cephalopod recruitment so variable? Heterogeneous conditions during the pre-recruit phase might be the source of inter-annual and spatial fluctuations in recruitment and abundance. Variations in growth can generate variations in the age/size-at-recruitment in cuttlefish (Challier et al., 2002).

Growth can be observed in many ways (Arkhipkin, 1991). Length-frequency analysis is one of them and has been applied in several studies on *L. forbesi* (Holme, 1974; Pierce et al., 1994b; Collins et al., 1995b, 1999). Most authors also point to the need for caution in interpreting such data, principally because length-frequency data on squid such as *L. forbesi* rarely allow clear identification of 'cohorts' (or micro-cohorts) that can be followed through time. This method is known to underestimate growth because of (a) mesh size selection of fishing gear, (b) immigration, and (c) the inter-individual variability in size at age (Caddy, 1991). Other techniques are the examination of periodic growth increments in hard structures such as the gladius or statoliths (Perez and O'Dor, 2000; Arkhipkin and Bizikov, 1991; Bizikov, 1991). In statoliths, the deposition of growth increments has been validated as daily in several squid and sepioid species (Jackson, 1994). In *L. forbesi*, the daily nature of statolith growth rings has been confirmed indirectly by Collins et al. (1995a).

Statolith ageing methods can give information on population parameters such as age structure and hatching dates. This is useful to better understand a key stage of the life cycle: the age when animals enter the exploited stage. Age at recruitment was assumed to be six months in the first study of this species' population biology (Holme, 1974). Although, several authors indicated that total life span could exceed the one year cycle presented by Holme (Collins et al., 1995a; Rocha and Guerra, 1999) the consequences of such observations on the timing of other stages remained unclear.

The present study investigates for the first time growth variations of *L. forbesi* during the pre-recruit phase in the English Channel and Scottish waters, using data collected in three different years. Such comparisons in growth are valid and of interest because populations in both areas seem to belong to the same 'genetic pool' (Shaw et al., 1999). Growth was estimated by the statolith ageing technique.

Our aim was (1) to obtain more information on the life cycle of squid *L. forbesi* in the English Channel and Scottish waters, especially on age-at-recruitment; (2) to analyse individual growth variability in order to answer questions such as: Are there inter-annual and spatial growth differences between cohorts? Within each cohort, do micro-cohorts show different growth patterns? Are such patterns consistent from year to year? Are fluctuations in recruitment correlated with growth variations? The relationship between fluctuations in recruitment and growth of pre-recruits is explored to test the hypothesis of density dependence in squid growth.

2. Methods

2.1. Sample collection

In the English Channel and Scottish waters, the selected sample sets were part of long-term biological sampling series. To study growth variations and the potential relation with recruitment in these two areas, inter-annual differences in landings were the criteria for the choice of years to be studied. From among annual cohorts sampled for biological data during previous research projects, we selected the years 1993, 1994 and 1998. French squid landings were considerably higher in 1993 and 1994 than in 1998, which suggested significant changes in population abundance.

In 1993 and 1998, monthly samples of *Loligo forbesi* were obtained from the Scottish fishery (Kinlochbervie port). In the English Channel, sampling was also on a monthly basis, samples being collected in the Port-en-Bessin fish market in 1993, 1994 and 1998. In both areas, biological samples were collected from commercial landings of offshore demersal trawlers which follow the same regulations about mesh size (100 mm) or minimal distance from the coast. Spatial variations therefore cannot have been caused by the fishing gears. In addition, statolith analysis concerned sub-samples taken in the same length range (<200 mm dorsal mantle length (DML)). Sub-samples of animals were selected from peak periods of recruitment. In the English Channel, recruits from April, June, July, August and September were studied. In Scottish waters,