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The energy accumulation of somatic tissue and reproductive organs in post-recruit female *Illex argentinus* and the relationship with sea surface oceanography

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ABSTRACT

The need to optimize limited energy between reproductive and somatic growth is a vital process for marine animals under variable oceanic environments, especially the cephalopod species with their short monocyclic lifecycle and environment-sensitive growth. In this study, the process of energy accumulated in somatic tissues and reproductive organs of post-recruit female *Illex argentinus*, an important world fishery cephalopod species, was investigated and its relation to sea surface oceanography was explored using generalized additive models (GAMs). During the course of sexual maturation, the somatic tissues and nidamental glands have a constant value of energy density, while the energy density of both ovary and oviducal complex increases significantly with maturity. Somatic tissues attain maximum energy at the physiologically maturing stage, decreasing slightly, but not significantly, thereafter. In contrast, the reproductive organs accumulate energy throughout sexual maturation. Additionally, the post-recruit female *I. argentinus* accumulates greater energy in somatic tissues and reproductive organs at lower surface temperature, higher chlorophyll-*a* concentration, a particular sea-surface height, and later month during the post-recruitment period. This evidence indicates that the reproductive effort is a continuum, and the interactions of sea surface oceanography might result in a higher level of energy accumulation in this species, which should assist future research of reproductive effort aimed at the strategy of spawning and subsequent recruitment processes of this species.

1. Introduction

Life-history theory predicts that organisms have to optimize the limited energy intake from their diet for the balance of reproduction and condition (Roff, 1983; Stearns, 1992), both of which are two extremely interdependent phenomena (Cortez et al., 1995). Energy fuelled into reproduction frequently distracts from somatic growth, while condition tends to influence breeding decisions or reproductive effort associated with reproductive success (Vleck and Vleck, 2002). The extent to which an organism invests nutrients in reproduction to the detriment of condition depends on the species concerned (Cortez et al., 1995), and is not fixed but varies with its own internal state and environmental variability (Calow, 1979; Lake, 1967).

Cephalopods are one of the major mollusk groups. Many species are short-lived (usually 1–2 years) and exhibit monocyclic reproduction and single-season breeding (Boyle and Rodhouse, 2005). Consequently, growth and maturation in these species is very fast and reproductive effort is relatively high (Collins et al., 1995). It is well documented that muscle is the major site for energy reserves in cephalopods (Castro et al., 1992; Guerra and Castro, 1994; Moltschaniwskyj, 1995), but sourcing energy for reproduction is strategy-specific. More and more findings show that spawning strategies amongst these species are driven by energy allocation to reproduction either from storing reserve in the muscle (i.e. capi-

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tal breeding) or ingesting food locally (i.e. income breeding) (Rocha et al., 2001). The former may result in a terminal spawning event (e.g. *Onykia ingens*(Jackson et al., 2004) and *Loligo vulgaris* (Sánchez and Demestre, 2010)), and the latter may allow individuals to spawn many times by steady and slow egg production (e.g. *Stenoteuthis oualaniensis* (Harman et al., 1989) and *Nototodarus gouldi* (McGrath and Jackson, 2002)).

Moreover, cephalopods are ready learners with environment-sensitive growth patterns, which allow them to adapt and explore new environments and to acclimatize to new situations (Boyle and Rodhouse, 2005; Vitti, 2013). And energy acquisition appropriate for a variable environment is ultimately important in determining the strategy for reproduction (Schreck et al., 2001). For example, the relative stability of a deep-sea environment but extreme oligotrophy may lead to reproductive strategies tending towards continuous spawning with low batch fecundity (e.g. *Rossia*, (Laptikhovsky et al., 2008)), or simultaneous maturation of a single batch of large eggs (e.g. *Pteroctopus tetracirrhus*, (Laptikhovsky et al., 2014)),whereas a shelf species might lay eggs in numerous batches over an extended period of time due to the high primary and secondary production of nutrients provided in a shelf water column (e.g. *Octopus Chierchiae* (Rodaniche, 1984)). Thus, it is likely that these species can regulate the processes of energy available for reproductive and somatic activities in response to environmental pressures within an overall reproductive strategy.

The Argentinean shortfin squid, *Illex argentinus* (Castellanos 1960) is one of the most important neritic squid species that distributes along the continental shelf and slope of the southwest Atlantic Ocean from approximately 22°S to 54°S (Haimovici et al., 1998; Jereb and Roper, 2010). Throughout these areas, at least four distinct stocks have been detected based on size and maturity structure, spawning season and hatching months (Haimovici et al., 1998; Jereb and Roper, 2010), but there seems to be little evidence of genetic difference between these stocks (Adcock et al., 1999; Carvalho et al., 1992; Roldán et al., 2014). Studies on marine ecosystems and trophic flows have shown that *I. argentinus* is a southern hemisphere example of a western boundary current species (Anderson and Rodhouse, 2001), and plays a key role in the southwest Atlantic ecosystem (Arkhipkin, 2012). Furthermore, it also supports the most important world cephalopod fishery in terms of landing tons (FAO, 2013), and most of the fisheries are conducted from the austral summer to early winter seasons in the Patagonian shelf paralleling 35°S and 54°S (Haimovici et al., 1998; Jereb and Roper, 2010).

This species has an approximate one year lifespan with females growing faster and attaining a larger size than those of males (Jereb and Roper, 2010). Its reproductive strategy is supposed to be the typical *r*-strategy, in which individuals have over 75000 oocytes of potential fecundity and lay eggs intermittently through one to two months (Laptikhovsky and Nigmatullin, 1993; Rocha et al., 2001; Rodhouse and Hatfield, 1990). During the period of post-recruitment in the feeding ground, this species undergoes simultaneous growth and maturation (Hatfield et al., 1992). This process is accompanied by an increasing shift of emphasis from somatic growth to reproduction, but is not associated with any degeneration of mantle muscle as there is no component of soma mass loss (Hatfield et al., 1992; Rodhouse and Hatfield, 1992), and there is no evidence of utilization of energy reserve to supply for gonad growth (Clarke et al., 1994; Schwarz and Perez, 2010). Therefore, the sourcing energy for reproduction could be directly from food intake as suggested by Hatfield et al. (1992) and Rodhouse and Hatfield (1992). However, a more recent study on the reproductive investment of this species has found that the reproductive development in females is at the expense of body muscle growth during the immature and maturing stages (Lin et al., 2015). Arkhipkin (1993) also reported that mature *I. argentinus* practically cease somatic

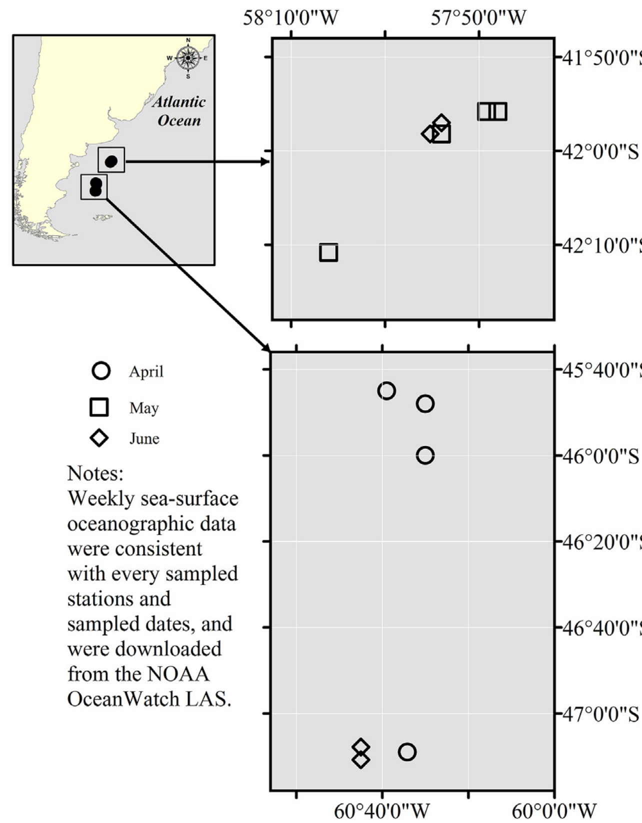

Fig. 1. Map of the studied area showing the sites of the sampled specimens of *Illex argentinus*.

growth, expending their energy on regenerative growth. Furthermore, even though both growth and maturation in this species are clearly linked to the thermal fronts and plankton production on the intermediate and outer Patagonian shelf (Bazzino et al., 2005; Portela et al., 2012), the process of energy accumulation in somatic tissues and reproductive organs in relation to surrounding environment has rarely been observed.

In this study, we investigated the energy accumulated in somatic tissues and reproductive organs of the post-recruit females from a major fishery stock, namely the South Patagonic Stock (SPS) (Haimovici et al., 1998; Jereb and Roper, 2010). The individuals of this stock have the largest size at maturity and spawn on slopes during the austral autumn (Haimovici et al., 1998; Jereb and Roper, 2010). Also, the relationship between energy accumulation and sea-surface oceanography is explored for better understanding the process. Under these analyses, we aim to expand our understanding of the process of energy accumulation and allocation to both somatic and reproductive growth, and to achieve novel insights into the reproductive allocation strategy in *I. argentinus* by, 1) determining the energy density of both somatic tissues and reproductive organs, 2) calculating absolute energy accumulation and its percentage with maturity, and 3) investigating the relationship between energy accumulation and sea surface oceanography during the period of post-recruitment in the feeding ground.

2. Material and methods

2.1. Sampling

Samples were taken on a weekly basis over three-consecutive months, from April to June 2014, in the high seas of southwest Atlantic (Fig. 1). All squid were collected from the commercial fishery landings. The sampling strategy was conducted to achieve