

Ontogenetic changes in mouth structures, foraging behaviour and habitat use of *Scomber japonicus* and *Illex coindetii**

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SUMMARY: The quick development of the skull structure is of vital importance to animals during the early stages of life given that herein are located the governing center and the mechanisms which make feeding possible. However, the rhythm of growth changes throughout the life cycle, a process which is particularly manifest in the proportionate head/body growth. The mouth structures grow proportionately to head growth. These accentuated changes in the anatomy of the animal could be reflected in its behavioural pattern (migrations between two areas in the case of some species and significant changes in diet connecting to these migrations). *Scomber japonicus* (Pisces, Scombridae) and *Illex coindetii* (Cephalopoda, Ommastrephidae) both undergo significant changes in the rhythm of growth of their respective mouth structures when they reach around 13-15 and 14-20 cm of total body length (mantle length in cephalopods) respectively. In *Illex coindetii* there are also differences by sex, being the changes of growth at 15 cm in males and around 20 cm in females. In both of these species, this change in the rhythm of growth implies a significant variation in diet as the consequence of a shift of habitat.

Key words: Ontogeny, *Scomber japonicus*, *Illex coindetii*, mouth structures, migration.

RESUMEN: CAMBIOS ONTOGENÉTICOS EN LAS ESTRUCTURAS BUCALES, COMPORTAMIENTO ALIMENTICIOS Y USO DE HÁBITAT EN *SCOMBER JAPONICUS* E *ILLEX COINDETHII*. – El rápido desarrollo del cráneo es de importancia vital durante las primeras fases de la vida del animal, ya que en él está localizado el centro rector y las estructuras que hacen posible la alimentación. El ritmo de crecimiento cambia a lo largo del ciclo vital y esto es especialmente evidente en el crecimiento de la cabeza en relación al del cuerpo. Las estructuras bucales crecen de acuerdo con el crecimiento de la cabeza. Los cambios anatómicos acentuados pueden quedar también reflejados en el patrón de comportamiento del animal (un cambio significativo en la dieta y en algunas especies, en relación con estos cambios en la dieta, son las migraciones entre dos áreas diferentes). *Scomber japonicus* (Pisces, Scombridae) e *Illex coindetii* (Cephalopoda, Ommastrephidae) sufren un cambio significativo en el ritmo de crecimiento de sus respectivas estructuras bucales: alrededor de 13-15 y 14-20 cm de longitud corporal (longitud dorsal del manto en cefalópodos) respectivamente. En *I. coindetii* hay también diferencias por sexos, siendo el cambio de ritmo de crecimiento a los 15 cm en machos y alrededor de los 20 cm en las hembras. En estas especies este cambio en el ritmo de crecimiento envuelve variaciones significativas en la dieta como consecuencia de un cambio de hábitat.

Palabras clave: Ontogenia, *Scomber japonicus*, *Illex coindetii*, estructuras bucales, migración.

INTRODUCTION

Food is one of the most important limitations to animal growth (WEATHERLEY and GILL, 1987). The characteristics of available food, quality, size, and accessibility will condition the trophic behaviour of

the consumers. The body morphology and growth, habitat, and animal distribution are in some way related to diet (WOOTTON, 1992). Trophic evolution necessarily produces a double specialization, which is, on the one hand mechanical (GALIS *et al.* 1994), in that it has to do with how the animal obtains, handles and ingests food and, on the other hand, biochemical (MARGALEF, 1981). There are two ways of

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originating an efficient feeding strategy; this is either obtained via time of evolution, as a result of natural selection, or it can be learned during the life cycle (HART, 1986). However, in the latter case, there must exist a previous construction (i.e. mouth structure) which allows for adequate exploitation of the food resources. Many species reveal morphological adaptations which are oriented to obtain food. They not only show the corresponding morphological adaptations, but also their behavioural patterns are totally influenced by the food type upon which they depend (EIBL-EIBESFELDT, 1979; WOOTTON, 1992). This adaptation is the consequence of the continuous interactions between the body/ behavioural development processes and external environment (HUNTINGFORD, 1986; GALIS *et al.* 1994). Examples of these interactions are represented in many taxa (invertebrates, fish, amphibians, reptiles, birds and mammals), where normally the juveniles and adults differ in their use of resources (WERNER and GILLIAM, 1984; WOOTTON, 1992; O'BRIEN, 1994).

Feeding, or to be more precise, the availability and accessibility of food, are just some of the reasons for many aspects of individual and social behaviour (GRANT, 1993) together with the spatial distribution of the species (WOOTTON, 1992; LIRMAN, 1994). Shifts in diet are often associated with, or caused by, shifts in habitat (WERNER and GILLIAM, 1984). Seasonal fluctuations of food resources force many species to make significant displacements during specific periods of their life cycles (MCKEOWN, 1984; WOOTTON, 1992). A migration between two habitats with different ecological conditions requires previous physiological and morphological characteristics and a new strategy of exploitation (MCKEOWN, 1984). The juvenile stages are more vulnerable to differences in environmental conditions between habitats (temperature, predation risk, food quality: HJORT, 1914), due to limitations imposed upon them by the level of body development, and most specifically the skull structures related to the mouth, and swimming capacity. These limitations will condition the trophic spectrum which will not be totally defined until the animal achieves the adequate body development.

In this paper, we document the existence of ontogenetic shifts in the diet and habitat of *Scomber japonicus* (Pisces, Scombridae) and *Illex coindetii* (Cephalopoda, Ommastrephidae). These ontogenetic shifts are related to previous morphological variations in mouth structures.

MATERIAL AND METHODS

This study is based on 721 individuals of *Scomber japonicus* caught around the island of Gran Canaria (14°00'N - 15°30'W) and 414 individuals of *Illex coindetii* caught on the continental shelf off Northwest Africa (from 14°11'N and 28°08'N). Mackerels were sampled from commercial catches using purse-seine and beach-seine nets between March 1988 and May 1989. Shortfin squids were obtained from the by-catch of bottom trawls for prawn and octopus, between August 1989 and April 1990.

Morphometric measurements were made to determine whether ontogenetic changes occurred in the structures used for feeding. The total body length (TL), lower jaw length and degree of mouth opening were measured for each fish (Fig. 1). The dorsal mantle length (DML) was also taken for each shortfin squid and the rostral lengths of the upper and lower beaks were also measured in 200 specimens (Fig. 2). All measurements were taken to the nearest 0.01 mm with a digital caliper. The stage of maturity and level of pigmentation of beaks were recorded from a subsample of 116 individuals of *I. coindetii* (55 males and 61 females).

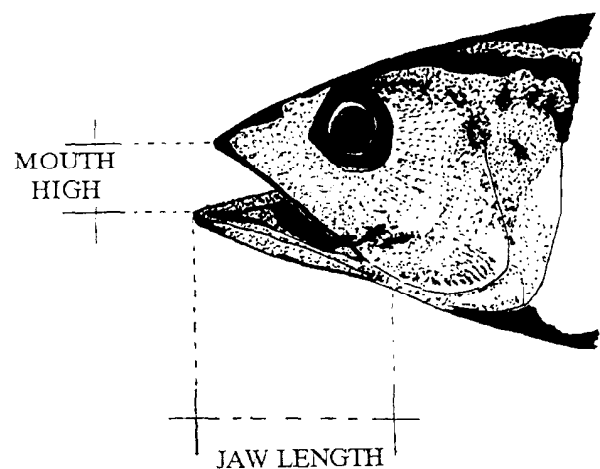
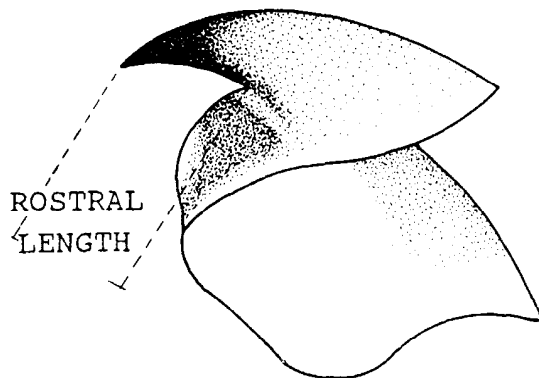


FIG. 1. – Measurement of jaw length in *Scomber japonicus*.

The stomachs of the fish and cephalopods were removed and preserved in 70% ethanol. All food items from the stomach were placed on filter paper to remove moisture and thereafter weighed. Prey items were identified to the lowest taxa possible. For each stomach examined, counts were made of the number of prey items in each prey category. An

UPPER BEAK



LOWER BEAK

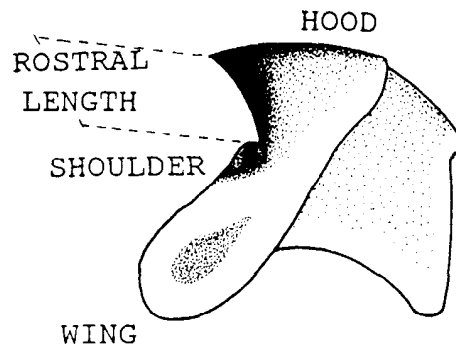


FIG. 2. – Measurement of rostral length in upper beaks of *Illex coindetii*.

index of importance by number (IN) for each stomach was calculated as the mean for each prey category, where $IN = ((\% \text{ composition by number}) \cdot (\% \text{ occurrence}))$ (WINDELL, 1971, VESIN *et al.* 1981) working on a scale of 100 where $\% \text{ composition by number} = \text{number species} \cdot 100 / \text{total number of all prey}$; and the percentage occurrence is the frequency of occurrence of a prey item in the stomach.

Wet masses were also determined for each prey category, and an index of the importance of each prey category by wet mass (IM) was calculated, where $IM = ((\% \text{ wet mass}) \cdot (\% \text{ occurrence}))$ (CASTRO, 1993) also working on the scale of 100, where $\% \text{ wet mass} = \text{wet weight species} \cdot 100 / \text{total wet weight all prey}$.

In general, small numerous prey items are important on account of their number whereas the heavy prey items, although found in scarce numbers, are important to the wet mass (HYSLOP, 1980). An index of total importance (TI) was calculated for each prey category as the mean value between IN and IM ($TI = (IN + IM) / 2$) working always on a scale of 100.

The hardness of the cephalopod beaks was established in relation to the degree of their pigmentation. The beak became harder the more it progressed in pigmentation (from non-pigmented to black brown). A scale of beak darkening ranks with growth was drawn for *Illex coindetii* and is to be found in Table 1.

A linear regression was established between lengths relating to mouth structures of *Scomber*

TABLE 1. – Scale of beak pigmentation in *Illex coindetii*.

DESCRIPTION OF LOWER BEAK DARKENING RANK
1 Only the rostrum and the anterior part of the hood are pigmented.
2 The pigmentation is only present in the rostrum and shoulder.
3 An isolated spot of pigment is present in the wings.
4 The initial pigmentation of the wings is in progress to the hood.
5 The initial pigmentation of the wings is finally joined to the hood.
6 The wings are completely pigmented but surrounded by a non-pigmented border.
7 The beak is fully pigmented in a soft brown colour.
8 The beak acquires an intense dark brown pigmentation.

japonicus and *Illex coindetii* and their respective body lengths (TL and DML). This allowed for points of significant change in the regression curve slope to be identified. The aim was to obtain the body size which corresponded to the greatest and most accentuated morphological change in the mouth structures. A comparison was then made between the slopes of the two sections of the regression line. After contrasting for heterogeneity in the variances per tracts of the curve (F test), we analysed the differences in the gradients with the result that we found the mean values of Y to be lower in one tract than in the other over a range of X values (MARTIN-ANDRES and LUNA DEL CASTILLO, 1990). A mathematical algorithm was drawn up to determine the significant variations (95% of significance) in gradient between tracts with one centimetre modification.

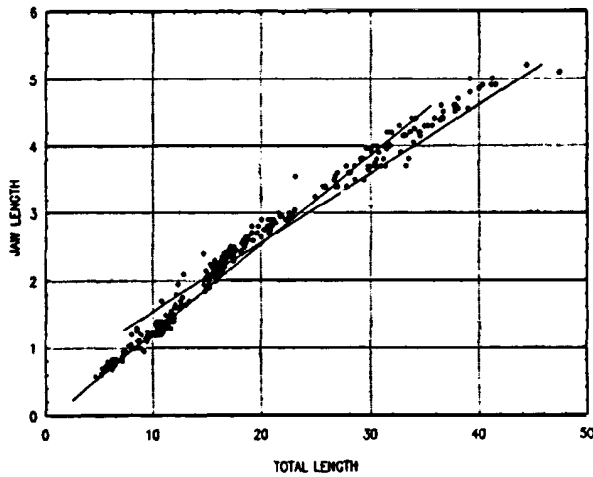


FIG. 3. - Linear regression between jaw length and total length in *Scomber japonicus* by sections.

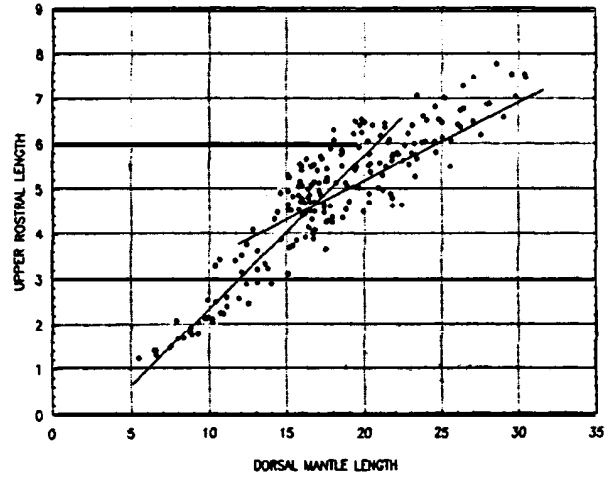


FIG. 4. - Linear regression between rostral length (upper beak) and dorsal mantle length (DML) in *Illex coindetii* by sections.

RESULTS

The linear regression analysis between the mouth structures and the body lengths (LT and DML) showed that *Scomber japonicus* undergo significant morphometric shift ($P < 0.05$) at around 13 to 15 cm TL (Fig. 3), while in *Illex coindetii* this significant morphometric shift is shown at around 14 to 20 cm DML (Fig. 4). However, when *I. coindetii* was separate by sex, we observed that the morphometric changes was obtained around 15 cm in males and 20 cm in females. This means that, at these sizes, an important change occurs in the rhythm of the growth of mouth structures (lower jaw in chub mackerel and upper beak in shorfin squid) of both species which is in direct relation to body growth.

Size-classes of both species were established

attending the morphometric, biological, ecological and fishery characteristics of the specimens. Three size-classes were identified in *Scomber japonicus*. The juvenile chub mackerel were defined as those fish ranging in size from 1.5 to 13.5 cm TL, immature fish as those ranging between 13.6 and 22.5 cm TL and adults as fish longer than 22.6 cm TL (CASTRO, 1993). These size-classes are similar to those used by WATANABE (1970) and ANGELESCU (1979) for *S. japonicus* from Japanese and Argentinian waters respectively. Individuals of *Illex coindetii* smaller than 12.5-15.5 cm DML (12.5 cm when male and 15.5 cm when female) were defined as juvenile-immature since it is considered that specimens are sexually mature after reaching these sizes (SANCHEZ, 1982) (Fig. 5). In the same way, specimens longer than 12.6-15.6 cm DML were identified as adults.

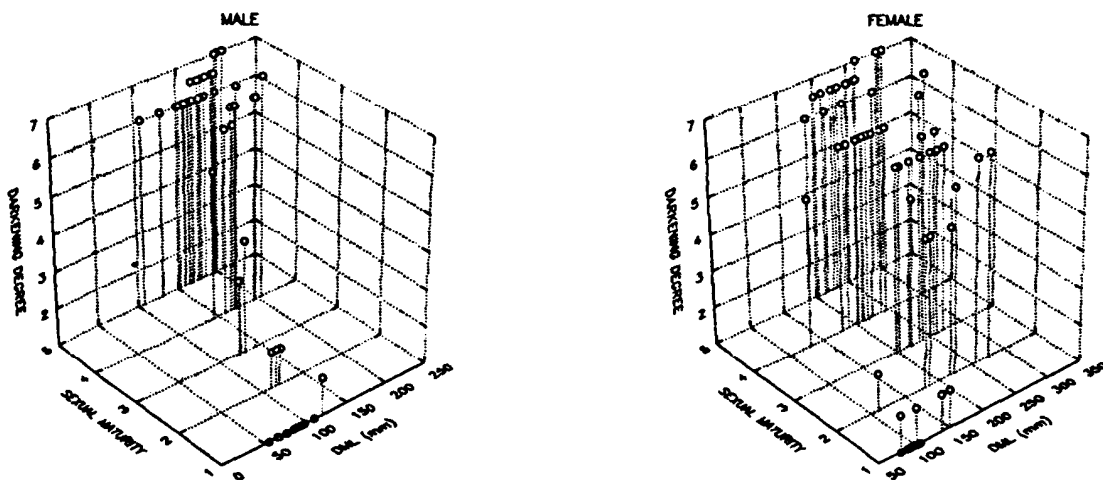


FIG. 5. - Three dimensional representation of darkening degree of lower beaks of *Illex coindetii* in relation with mantle growth and maturity (55 males and 61 females).

TABLE 2. – The food taxa and dominant species found in the stomach of *Scomber japonicus*.

1. CHAETOGNATHA
2. POLYCHAETA
3. CLADOCERA
4. OSTRACODA
5. COPEPODA
Oncaea sp.
6. AMPHIPODA
Dexamine sp.
7. ISOPODA
Idotea sp.
8. CUMACEA
9. MYSIDACEA
Gastrosaccus normani
Anchialina agilis
10. STOMATOPODA
11. EUPHAUSIACEA
Euphausia spp.
12. DECAPODA
13. GASTROPODA
14. LAMELLIBRANCHIATA
15. CEPHALOPODA
Ommastrephes bartrami
16. APPENDICULARIA
17. PISCES
Sardina pilchardus
Macroramphosus scolopax

The diet of chub mackerel in the area of the Canary Islands was made up of 17 taxonomic groups (Table 2). Copepods and mysids were the dominant prey (27.0% and 24.5% respectively). Fish were less frequent in the diet but their importance in the mass was moderately high. The diet of juveniles was dominated by fish fry (24.7%) and small prey such as copepods and appendicularians. Copepods and appendicularians were the main component of the diet (26.6% and 17.5% respectively) decreasing in importance proportionate to fish size. Immature specimens presented a diet based on copepods and mysids (32.9% and 20.9% respectively). The contri-

TABLE 3. – The food taxa and dominant species found in the stomach of *Illex coindetii*.

1. AMPHIPODA
2. EUPHAUSIACEA
Thysanopoda sp.
3. DECAPODA
Plesionika spp.
Pasiphaea sivado
4. CEPHALOPODA
Sepia sp.
Sepia bertheloti
Loligo sp.
Alloteuthis sp.
Abralia veranyi
Illex coindetii
Todaropsis eblanae
Octopus sp.
5. PISCES
Maurolicus muelleri
Diaphus dumerelli
Epigonus telescopus
Dentex spp.
Diplodus spp.
Microchirus boscanion
Solea spp.

bution of fish in the diet of immature chub mackerel was not significant (2.05%). Mysids, copepods and fish were the most important prey in the diet of adult chub mackerel (27.4%, 18.0% and 13.2% respectively) (Fig. 6).

The differences between the diets of juvenile, immature and adult chub mackerel are to be seen in the shift from small fish and copepod prey to mysids and copepods in fish lengths over 13.5 cm TL, and thereafter to mysids and fish for adults over 22.5 cm TL.

The trophic spectrum of *Illex coindetii* was made up of 5 taxonomic groups (Table 3). The diet of juvenile-immature of *I. coindetii* was mainly fish (45.09%) and cephalopods (20.19%), and in a lower proportion decapods (21.10%), euphausiids

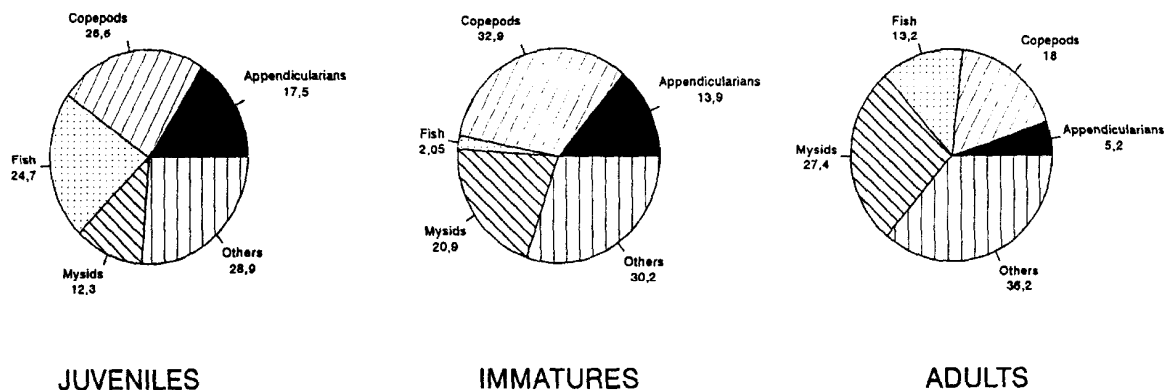


FIG. 6. – Proportion of most important prey items in the diet of juvenile, immature and adult *Scomber japonicus*.

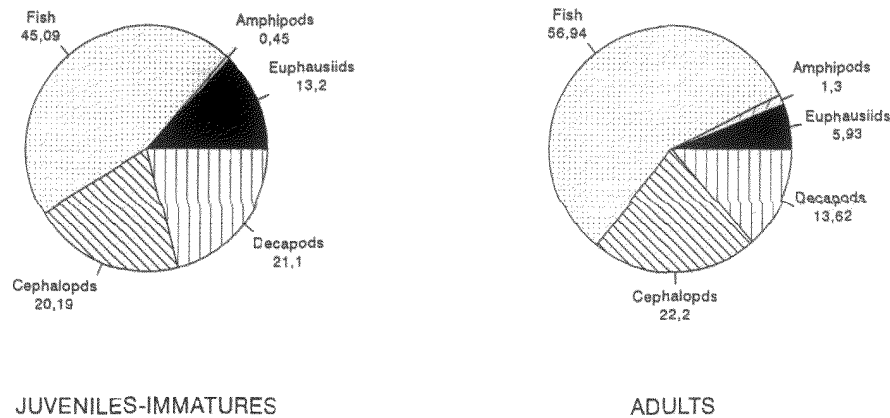


FIG. 7. – Proportion of most important prey items in the diet of juvenile-immature and adult *Illex coindetii*.

(13.20%) and amphipods (0.45%). Although adults also showed a preference for feeding on fish (56.94%) and other cephalopods (22.20%), they also consume decapods (13.62%) and euphausiids (15.93%) showing a minor predation on amphipods (1.3%) (Fig. 7).

Figure 5 shows that at around 12-15 cm DML, the beak of *Illex coindetii* began to be pigmented (this also relates to the degree of hardness of the beak) which also coincides with the beginning of sexual maturity in males, and to a lower extent in females.

DISCUSSION

The specific genotypic characteristics condition the phenotypic evolution of behaviour which will also be modulated by two important parallel processes in mutual interaction. The first is the development of the anatomical structures which are indispensable for the expression of a determined behaviour (HUNTINGFORD, 1986). Genetic heritage allows for some simple motor schemes to be expressed and organized in more complex sequences, which are highly elaborate and of greater or lesser diversity, according to the environmental stimulus. At this moment the second process becomes of importance i.e. experience. This will also be expressed as a function of the environmental elements (ecological and social) of the context in which the individual is inhabiting (MANNING and DAWKINS, 1992). There is no doubt that individual maturity is also dependent on environmental factors, above all, on food.

Ontogenetic changes in diet are common in fish

(ROSS, 1978; MITTELBACH *et al*, 1988; UIBLEIN, 1991; LIRMAN, 1994; MOOKERJI and RAMAKRISHNA-RAO, 1994) and appear to function as an adaptation in order to maximize energy intake, thereby decreasing the risk of predation (IVLEV 1961; WEATHERLEY, 1972; GROSSMAN, 1980; WERNER and GUILLIAM, 1984; WERNER and HALL, 1988) and/or as a mechanism of expanding niche width and minimizing intraspecific competition (KEAST, 1977). From the results obtained, we can infer that there is an ontogenetic shift in the habitat and diets of *Scomber japonicus* and *Illex coindetii* which relates to a previous morphological shift in mouth structures. An important development of the mouth structures (morphology and vigor) allows for more effective predation on large prey. These shifts in the body structures are continuous through the life history from the pre-larva to the adult stages, but during specific periods of the life cycle these morphological shifts are more accentuated (BAS, 1964; BAS and MORENO, 1993; GALIS, 1994). The ontogenetic shifts of habitat are often correlated to discrete growth periods in the life history which, in some cases, are attributed to a change in food characteristics (WERNER and GILLIAM, 1984).

Generally juveniles live in temporarily rich areas (nursery areas) (ZIJLSTRA, 1972; MANN, 1982) with limited carrying capacity where the available food is strongly influenced by the seasons, such as in coastal areas. Before food begins to be scarce, the juveniles should be ready anatomically to migrate to other more profitable areas, especially in all aspects referent to structures and features of vital importance (mouth structures, vision, fins, swimming resistance, etc) which will allow the animal to

be competitive in the new ecological conditions. Possibly, these morphological shifts are not totally apparent in all species (GROSSMAN, 1980). Perhaps the species which do not need to migrate (BAS and MORENO, 1993) do not undergo significant shifts in their prey size (WERNER and GILLIAM, 1984). These shifts are recorded in the genetic codes (with a permanence in time which is far superior to the environmental changes which the individual suffers during its life cycle). In the case of fluctuating environmental conditions in the nursery habitat (vital space, inter and intraspecific competition and predatory risk and specially available food), the species search out two possible answers: a higher degree of specialization (BERGMAN and GREENBERG, 1994) or migration to other more profitable areas (MCKEOWN, 1984). Two examples of these ontogenetic behavioural changes in the marine species are *Scomber japonicus* and *Illex coindetii*, species which migrate (daily and/or seasonally) during their life history, and most especially in the adult stages (SCHAEFER, 1980; DAWE and BECK, 1985; ARKHIPKIN and FEDULOV, 1986; BRUNETTI and IVANOVIC, 1992).

Juveniles of chub mackerel live in coastal waters feeding on small crustaceans (especially copepods) although their voracity and mouth structures allow them to prey on other fish species (HUNTER and KIMBRELL, 1980; CASTRO, 1993). This stage of growth is particularly rapid and is to be noted, above all, in the head growth (LORENZO, 1992). The coastal area of the Canary Islands is an unstable environment with a limited carrying capacity and is strongly influenced by seasonal cycles (BAS and MORENO, 1993). The important concentration of juveniles of many fish species found during the first half of the year in the coastal ecosystem produces a critical situation in the carrying capacity. At the end of this period, juveniles of chub mackerel have reached 14 cm TL and are ready to migrate offshore and to show efficient predation on the mysids which swarm during the night (individuals of 14 cm TL were not found in catches, probably due to this migration offshore). Subsequently, when fish are sexually mature, they migrate again, once yearly and coinciding with spawning, between the feeding area of adults and the spawning area (BAIRD, 1977; CASTRO, 1993).

Immature specimens of *Illex coindetii* manifest a higher proportion of euphausiids in the diet than adults, which would tend to suggest a major relationship with the pelagic domain (DAWE and BECK, 1985; ARKHIPKIN and FEDULOV, 1986; BRUNETTI and

IVANOVIC, 1992; ARKHIPKIN and LAPTIKHOVSKY, 1994) where these crustaceans are abundant at night (RUBIES, 1976; LAPTIKHOVSKY, 1989). In the first stage and before reaching sexual maturity, shortfin squids undergo suitable morphological transformation which will allow them to make significant vertical displacements during the night-day (ARKHIPKIN and LAPTIKHOVSKY, 1994), and even possible longitudinal spawning migration as reported in *Illex illecebrosus* (O'DOR, 1987). This morphological shift implies an adaptation to fast swimming (significant increase in the mantle cavity and perfection of fin structures) (ARKHIPKIN and FEDULOV, 1986). At the same time, their mouth structures (beaks) become harder and the animal adapts to catching faster prey and escaping quickly, apart from which they have enough strength to break up hard fish structures. On the other hand, adults prey on other cephalopod species and fish, especially fishes of the genus *Microchirus*, that are abundant in the stomach contents of adult shortfin squids. This fish inhabits sand or muddy-sand bottoms (FISCHER *et al*, 1981). This means that adults of *I. coindetii* are associated with the sea bottom during the day time, as reported by ROPER and SWEENEY (1981) and MANGOLD (1983). The major presence of benthic amphipods in the diet of adults corroborate this major dependence with the sea bottom. Adults make significant vertical displacements in the water column at night where they feed on myctophids (OVCHAROV *et al*, 1985; CHESALIN, 1987) and other pelagic cephalopods. The possibility exists that *I. coindetii* migrate to higher latitudes coinciding with spawning as was observed in *I. illecebrosus* in the Northwest Atlantic (O'DOR, 1987) which spawn directly on the sea bottom.

The ontogenetic shifts experienced by animals are important for guaranteeing the survival of the species under changing environmental conditions. Corporal development shaped according to the genetic code of the species and expressed in phenotypic characteristics allows the animal to face the basic conditions of its environment. However, the anatomical structure as described by the genes reveals very little flexibility and would not facilitate (*per se*) the survival of individuals in a situation of environmental fluctuation. This genetic rigidity is compensated by the ontogenetic shift in behaviour as a complex response to these environmental fluctuations. However, as explained by HUNTINGFORD (1986) a specific behavioural pattern will only become manifest when the anatomical structure required for its development is already present.

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