SILVERING IN THE EEL: CHANGES IN MORPHOLOGY, BODY FAT CONTENT, AND GONADAL DEVELOPOMENT

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Abstract

The commonly used criterion of maturing degree of the eel is skin color, with immature adults as ‘’yellow eel” and maturing adults as “silver eel”. The process of metamorphosis in eel is thus named “silvering”. In eels, the common characters of silvering process are accompanied by morphological (e.g. color and thickness of integument, eye size, body length and weight, size of pectoral fins) and physiological (e.g. age at maturity, digestive tract, visual pigments, composition and function of skeletal muscle, swim bladder structure, locomotory behavior, density of chloride cells in the gill) modifications, together with the development of gonads. These modifications are beforehand preparation for the future spawning migration in the environment of deep sea. The knowledge about the phenomena occurring in eel silvering comes mainly from studies in temperate eel species, namely Japanese, American, and European eels, and this review is mainly concerned on the morphological and gonadal changes during the silvering of eels.

Keyword: eel, silvering, metamorphosis, reproduction, migration

Introduction

The life history of the catadromous eel, genus *Anguilla*, is very complicated and distinctive. The eel spawns in the deep tropical/subtropical ocean. Their leaf-like larvae, leptocephali, are transported and dispersed by ocean currents, and metamorphose into glass eels after several months of drifting. Glass eels become pigmented elvers in the estuary and grow in freshwater until silvering. Eels undergo a complex series of morphological and physiological changes as they metamorphose from freshwater yellow form to seagoing silver form in preparation for spawning migration. Morphological changes associated with this process include a change in skin color from yellow to silver/bronze (1), integumental thickness (1,2), increased eye size (3), increased body length and weight (1,4), shape of pectoral fins and snout (1). On the other hand, physiological changes include the degeneration of digestive tract (5), changes of visual pigments (3), modification in the composition and function of skeletal muscle (6), alternation of swim bladder structure (7), change of locomotory behavior (4), higher density of chloride cells in the gills (8), and gonadal development (9).

The metamorphosis of eels from ‘‘yellow’’ to ‘‘silver’’ stage could be regarded as the onset of puberty. In teleost, puberty is the period during which a juvenile acquires the capacity of reproduction for the first time. It starts with the spermatogenesis in the male and oogenesis in the female, and ends with the spermiation and ovulation in the male and female, respectively (10,11). For eels, the development of gonads is quiet for many years till the onset of silvering, but is limited to the beginning of gametagenesis with low GSI. Furthermore, if silver eels are kept in aquaria, they do not undergo further sex maturation. The sexual blockage at silver phase seems to exist in all eel species, though with various levels of constraint among species (12).

Due to rapid development of the eel aquaculture industry in Southeast Asia countries, elvers in the estuary were over exploited, which have severely influenced the recruitment of the eel in the river. Therefore, it’s important to develop artificial propagation to sustainably supply elvers for aquaculture to reduce the fishing pressure of the eel. However, little is known about the reproduction biology of the eel, as sexually mature eels have never been caught in the wild, and silver eels do not complete gonadal development in the captivity condition. Thus, hormonal treatment is the only approach to induce advanced gonadal development. Experiment to successfully induce spawning of Japanese eels dates back to 1974 (13). Unfortunately, the larvae obtained usually did nor survive long (253 days reported by Tanaka, in

Japan), and did not grow into glass eels. Hence, in order to provide proper management policy of eels (e.g. setting up fishing-forbidden seasons) and aid artificial propagation (e.g. the choice of eels for artificial maturation), it is helpful and necessary to better understand the silvering phenomena and mechanisms of the eel. In this review, we focus on the comparison of silvering phenomena among anguillid eels according to the results of our study and published papers, and the possible roles of these changes during silvering are discussed.

Migration in silver eel

It is generally accepted that the eel starts downstream spawning migration after metamorphosing from ‘‘yellow’’ to ‘‘silver’’ eel. The silver eel may migrate as long as thousands of kilometers back to its spawning ground [(1)]. For example, the Japanese eel is supposed to spawn in the North Pacific Ocean west of the Mariana Islands, which is more than 3000 km away from the continental shelf of Asia [(14)]. In European eel, the distance may be over 6000 km from Europe mainland to Sargasso Sea, the inferred spawning area [(15)].

The temperate eels usually have similar migration seasons. From our investigation results, silver Japanese eels occurred in late autumn and winter (Table 1). In European eel, the migration activity starts in August, peaks in September/October, and declines in January/February [(1)]. In American eel, it migrates peaks between late August and mid- November [(16)]. In addition, for New Zealand longfin and shortfin eels (*A. dieffenbachii* and *A. australis*, respectively), migration occurs in March and April, about the late autumn in southern hemisphere [(17)]. These results indicate that the migration time of silver eels occur mainly in autumn and winter for temperate species

In fishes, reproductive processes often exhibit endogenous rhythms controlled internally and externally. The external environmental cues that are used more commonly are light period and temperature [(18)]. In temperate zone, since the seasonal changes of these two factors are significant, they could be used as the silvering triggers by the temperate eels for synchronization of their reproductive activity. However, the mechanism is still unclear and remains to be further investigated.

Feeding or not during silvering

Whether the eel continues or stops feeding during silvering remains controversial. In European eel of yellow stage, the seasonal variations in appetite show that the food intake of the eel increases in March, peaked in summer, and then declines during autumn following by a winter fast of several months which may be due to the lower water temperature [1,19]. Since the silvering seasons of the eel coincide with those of declining food intake, and silver eels have regressed digestive tracts [4], it is generally accepted that silver eels do not feed. Our results also showed that silver Japanese eels have regressed digestive tracts. However, Beulleus *et al.* [20] observed that cultured male eels continue to eat and grow in silver stage, although with poor appetite. In addition, Dollerup and Graver [21] found that after repeated induction of testes maturation with hCG to induce spermiation in male silver eels, they are then given food and the food intake gradually increase and eels grow both in size and weight. Their atrophied alimentary tracts regenerate. This suggests that, at least in the males, the reversibility of digestive function is possible.

Marchelidon et al. [22] found that silver eels with naturally fasting present a more significant regression of the digestive tract than that of yellow eels with experimental starvation. Pankhurst and Sorensen [23] indicated that starvation alone does not result in gut degeneration in sexually immature European and American eels, but gut significantly degenerates in silver and hormone-injected sexually mature eels. These results suggest that the regression of alimentary tract in silver eel may be hormone-triggered, not only because of fasting. In natural condition, it is more possible that under the effect of endocrine during silvering, the appetite of silver eels were inhibited, but the status might be reversible.

Size and age at first maturity

In European eels, the size of silver eels was estimated to be 35-41 cm for males and 54-61 cm for females, and the age of silver eels ranged from 8-12 years in females, and from 6-9 years in males [1]. In Japanese eels, our study showed that they reached silver stage at the length range of 45-61 cm in males and 50-79 cm in females (Table 1). Tzeng et al. [24] found that the mean ages of silver Japanese eels were 6.4 and 8.3 years in the male and female, respectively. In American eels, the size and age of silver eels were 35-47 cm and 12.7 years for males, and were 40-94 cm and 19.3 years for females [16]. The common phenomenon derived from these studies is that the male eels enter silver phase in younger age and shorter body length than female eels.

The differences in age and size between silver male and female raise a question— which factors correlate to the onset of silvering? The body size? age? or both? For American eels of silver stage distributed between Georgia and Newfoundland, the ratio of maximum to minimum values was 1.6 for body length and 2.7 for age [25]. In European eel of northern and central waters, silver male eels were slightly older (average about 1.5 years) than those from southern Europe. The age difference between females was even greater. The average length, however, did not differ to the same extent [1]. In addition, Beulleus *et al.* [20] reported that European silver eels occur at earlier ages in hatchery conditions than in natural environment. Hence, these results infer that the silvering of eels seem to be more related to size than to age.

Tzeng *et al.* [24] found that the growth rate of the females at juvenile stage has no difference to that of males, and it is well known that the size at maturity is shorter in males than in females. If the onset of silvering was size dependent for each sex, then the mean age at maturity should be younger in males than in females. This is proved to be true as described previously (Table 1). On the other hand, Vølleatad [26] indicated that the age at first maturity was negatively related to growth rate. That is, eels with better nutrition might become sexually mature earlier than those with poor nutrition. This could partially explain the variety in the age of silvering.

Sex ratio

Ontogenetic development of the eel is very complicated, and the mechanism of its sex determination is still unclear. In European eel, Karyotypes studies failed to identify heteromorphic sex chromosomes [27], and descriptions of gonadal differentiation met various contradictory opinions: the primordial gonad passes through an intersexual phase, either a female or a male phase; the primordial gonad of a female phase; or a testis-like primordial gonad phase [20]. It is thus difficult to determine the sex of the eel at early life stage. In natural environment, European eels show a variable sex ratio, ranging from almost complete males to predominantly females. It is commonly believed that males prefer living in estuaries and brackish lagoons, and females are found mainly in freshwater [1]. Sinha and Jones [4] raised a possible explanation for this phenomenon. If sex is determined metagamically, then on arrival all elvers are all asexual. Their migration is random and their sex is determined by the environmental cues in which they grow up. That is, freshwater environment may prefer the development of female sex, while brackish water one, on the contrast, may favor the development of male sex.

In culture ponds, where eels are usually reared in high density, males predominate significantly. On the other hand, glass eels could be feminized by feeding them estradial-17β [28]. These results indicate that the eels might possess bi-directional potential of sex development. Consider the situation happening in natural and cultural conditions, density may be a major role for eel sex determination. How the signal of density is translated and processed to affect sex differentiation remains unknown. Maybe eels in crowded population suffer higher pressure (in cultured ponds) or lower food availability (in natural environments), which would modify the endocrine condition and thus affect the sex determination cascade of the eels toward the males. In contrast, if the space was spacious and/or the food was plenteous, they might prefer sex differentiation toward the females.

Morphological changes during silvering

In silver stage, the ocular index (OI) of European eel was $\leqq$ 6.5 in the sexually immature adults, and $>$6.5 in the sexually mature ones [3]. In cultural capacity, silver females and males of European eel had OI of $>$7.2 and $>$6.2, respectively [20]. On the other hand, the mean OI in sexually maturing American eels usually precede 6.0. In our investigation, the ranges of OI of Japanese eel were between 3.2- 6.9 and 3.7-5.8 in silver females and males, respectively (Table 1), and which was highly correlated to GSI (Rsqr=0.65, data not shown). Compared to the silver European and American eels, the silver Japanese eel in Taiwan has smaller mean OI, which may be due to species-specific difference. Despite the change in eye size during silvering, the visual pigments of European eel are also modified, with increased numbers of rod cells and decreased numbers of cone cells [3]. On the other hand, the FI of Japanese eel in our study showed significant increase in silver stage but was highly overlapped among maturation stages, thus no a clear-cut point could be defined (unpublished). What is the benefit to have larger pectoral fins and eyes for silver eels? It is well known that eels have to migrate long distance to reach the spawning area. It is thus reasonable to suppose that larger pectoral fins may add swimming ability. Similarly, the large eyes and rich of rod cells in retinas are also adaptive to dim environment. Hence, these modifications could be regarded as beforehand preparation for the demand of future spawning migration in the environment of deep sea.

In Japanese eel, opposite to the similar change tendency of the ocular and fin index in both sexes during silvering, the mean HSI increased significantly in silver females but not in silver males (unpublished). Bertin [29] indicated that eels accumulate fat in muscle and liver during growth. In addition, during the vitellogenic process, the oocytes uptake yolk precussor, vitellogenin (VTG), from the blood. VTG is produced from the liver in response to estrodiol [30,31]. This suggests the translocation of energy, especially the fat, from muscle and liver tissues to the gonads. In female Japanese eels of silver stage, deposition of large amount of oil-droplets and small amount of yolks in oocytes are actively in progress, which needs the involvement of liver. It may be the cause for the livers to become larger in females during silvering, and is reflected on the increasing HSI. On the other hand, no significant change of mean HSI was seen in silver Japanese males (unpublished), as they did not accumulate oil-droplet and vitellogenin in spermatogonia, and their testes are still growth-arrested.

Development of gonad during silvering

During silvering, the GSI of male New Zealand longfin eel (*A. dieffenbachii*) and shortfin eel (*A. australis*) in non-migrating stages is less than 0.05%. Spermatogonia are seen in the small nests with 2 to 4 cells [32]. In migrant shortfins, GSI moderately increases to 0.20% with spermatogonia mainly in type A and B stage, only a few spermatozoa are occasionally observed. On the other hand, migrating longfin males have much-increased GSI (0.96%), and spermatozoa are seen in the testes of the majority (83%). In American eel (*A. rostrata*), the mean GSI of the silver males was 0.63%. The testes have well- defined tubules with distinct lumens lined with spermatocytes and spermatogonia [2]. In European eel maintained in captivity, intersex yellow eels and male silver eels have relatively low GSI between the range of 0.01-0.04 and 0.03-0.29, respectively [20], and the formation of tubules with clear lumina is the only criterion to discriminate between these two phases. Colombo *et al*. [9] indicated that in European eel, the germ cells of some nests in yellow stage are mainly in mitosis, and single oocyte is found in all section. Secondary spermatocytes and spermatids are not observed. In silver males, however, nests of spermatids and spermatozoa are present in almost all testes. These results show the high variety in development status of testes during silvering between different eel species. In our study, the GSI in males ranged between 0.03-0.25 without statistical difference among these three developmental stages (Table 1). Although the GSI was low in all stages, spermatogenesis was active (data not shown). The increasing number of type B spermatogonia took the place of connective tissues during silvering process. In silver males, spermatids, spermatozoa, and single oocyte were never observed. These results suggest that the testes of silver males in Taiwan are still in early stage of spermatogenesis comparing to other eel species.

Unlike the low degree of development in male testes, there is significant enlargement in oocyte diameters during silvering, and the rapid developments of ovaries coincide with the morphological changes. The oocytes often enter oil-droplets stage and sometimes even vitellogenetic stage, thus result in rapidly increase of GSI. In previous studies, the GSI in migratory females vary from average 1.5% in *A. anguilla*, 2.0% in *A. japonica*, 2.8% in *A. bicolor bicolor*, 3.3% in *A. australis*, and 7.2% in *A. dieffenbachii* (33) (Table 1). In American eel, it ranges between 1.62-3.48 due to different collection areas (16). In our study, the GSI for silver Japanese females ranged between 0.69-2.24% (mean 1.33±0.08%, Table 1), somewhat lower than previous study in Japanese eel and was comparable to European eel. Why are the mean GSI of Japanese and European eels lower than other anguillid eels? We suppose that the degree of gonadal development in silver eel before migration should be inversely correlated to its migratory distance. In European eel, the distance is over 6000 km from Europe mainland to Sargasso Sea, the supposed spawning area (15). In Japanese eel, the distance is longer than 3000 km from Asia mainland to inferred spawning ground, the North Pacific Ocean west the Mariana Islands (14). Such long distance migration would take a few months for eels to reach there. It would be thus ‘‘energy wasteful’’ to trigger gonadal development early before it's spawning time, and evolution may thus favor low-degree developments of gonads for eel species that have to migrate long distances. If our speculation was correct, then we could predict that migratory distance may be longer in European and Japanese eels with lower mean GSI in silver stage, and is shorter for eel such as *A. dieffenbachii,* which has larger mean GSI in silver stage compared to other anguillid eels (Fig. 1). However, it needs to make clear the other anguillid eels' spawning area to clarify this hypothesis.

Energy stores and the onset of silvering

In 1974, Frisch and McArthur (34) raise the weight hypothesis of the onset of puberty, indicating that puberty occurs when body weight reaches a certain level. This hypothesis is then modified by Ronnekleiv *et al*. (35), who suggests that puberty is probably induced when fat stores, not weight itself, reach a certain level.

For eels, they usually cease feeding in silver stage and have to migrate long distance back to their spawning ground. The energy required for migration and gonadal development thus depends totally on large amount of fat accumulating in the body. From this point of view, it is reasonable to suppose that the migration in silver phase may need a minimum level of fat reserves [36]. The hypothesis is also supported by our study in Japanese eels. The fat stores in muscle range between 13-25% (mean 18%) in the silver stage (Table 1), and the lowest limit of silvering is 13% in both sexes. However, Svedäng and Wickström [37] found that the silver European eels of few sampling areas have mean muscle fat content lower than 10%, some specimens have fat stores even as low as 1%. They suggest that the maturation process in eel may be more flexible than were thought before, and migration together with gonad development might arrest temporarily and resume feeding to accumulate enough fat reserves before migration starting again. Since the eel stage was judged only by visual inspection in their study without gonadal histology and data of morphometric index, error judgment of stages might occur and result in the underestimation of fat content in silver eels.

Conclusion

The classification of maturation stages of the eel can be done by the silver color of the skin, changes of the morphometric indexes, or gonadal histology. The changes of these characters usually couple together during silvering (Fig. 2). The silver eel, though enters the puberty, remains in the pre-maturation stage. In addition, the male eels enter silver phase at a younger age and shorter size than the females, which may be the result of sex-related difference in growth pattern. The simultaneously changes in morphology and physiology are thought to be a biological pre-adaptation of the spawning ground in deep sea. To better understand the whole views of silvering of eels, it is necessary and helpful to integrate studies from different fields, e.g. molecular biology, endocrinology, physiology, and ecology.

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Figure legends

Figure 1. Hypothesis of the relationship between female GSI and migration distance. Abbreviation: AA, A*nguilla anguilla*; AJ, *A. japonica*; AR, *A. rostrata*; AD, *A. dieffenbachii*. The numbers inside parentheses indicate the GSI and distance, respectively.

Figure 2. Changes in morphology and physiology during silvering.

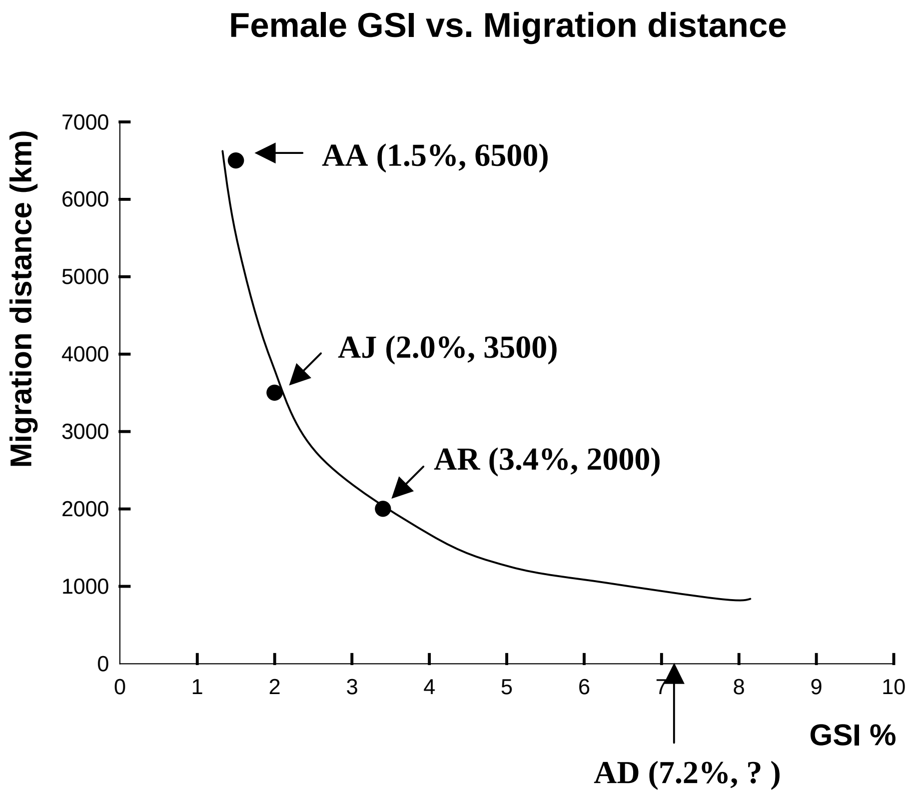
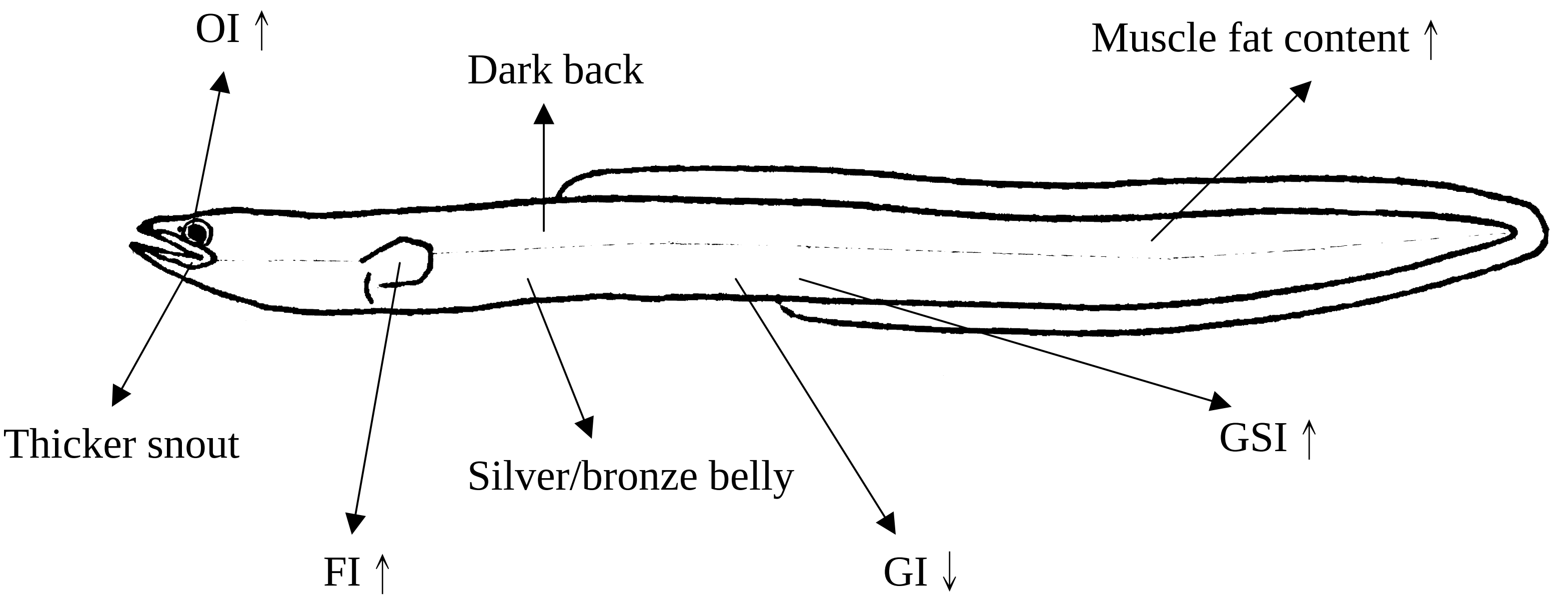

Female GSI vs. Migration distance
Migration distance (km)
7000
6000
5000
4000
3000
2000
1000
0
0
1
2
3
4
5
6
7
8
9
10
GSI %
AA (1.5%, 6500)
AJ (2.0%, 3500)
AR (3.4%, 2000)
AD (7.2%, ?)

Fig. 1


OI ↑
Dark back
Muscle fat content ↑
Thicker snout
Silver/bronze belly
GSI ↑
FI ↑
GI ↓