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Evolution of cannibalism in the larval stage of pelagic fish

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Abstract. Larvae of several ocean pelagic fish species, such as tunas and marlins, have been known to have large jaws, but the ecological significance of this unique morphological character has been hardly analyzed in evolutionary ecology. Pelagic spawners produce small and nutrition-poor ova, and spawning and nursery grounds of the open ocean migratory fishes are oligotrophic. We hypothesize that cannibalism would be a possible life style in the larval period and the large mouth gape would be an adaptive morphological characteristic for a cannibal in the oligotrophic pelagic environment. We showed that mouth gape size of the open ocean pelagic fish is significantly larger than that of offshore/coastal pelagic fish in larval period. A mathematical model demonstrated that cannibalism would tend to evolve in high sea environment. Our findings suggest an evolutionary pattern of cannibalism trait in the larval stage of pelagic fishes.

Key words: cannibalism, high sea, invasibility analyis, larval period, pelagic fish

Introduction

Evolutionary biology have been developed by using several taxonomic groups of animal and plant (Ridley, 1996). Expanding our knowledge about life history of organisms not only in terrestrial but also in aquatic fauna is important to be robust the evolutionary theory. Pisciformes is one of the most successful groups in aquatic environment. Even though taxonomists recognize roughly thirty thousand fish species, our knowledge about their behavior, morphological development and life history is very limited. Information about ocean fish is fragmentary. Particularly, early stage selection pressures are hardly known for most marine fishes.

Cannibalism had been a phenomenon that is not well rationalized by formal evolutionary theory. A real observation of cannibalism in an organism makes us believe that natural selection designed it, or leads us to consider that it is an abnormal behavior in the particular circumstance. In theoretical side optimal diet choice and density dependent population regulation are thought as causal factors governing cannibalism evolution (DeAngelis *et al.*, 1979; Elger and Crespi, 1992; Fox, 1975; Polis, 1981; Stenseth and Reed, 1978).

It is considered that cannibalistic behavior might often evolve in environments of low food availability with hunger and starvation (Elger and Crespi, 1992; Folkvord, 1997; Fox, 1975; Polis, 1981). It has been shown in several studies that the role of cannibalism is reduced in the presence of sufficient quantities of alternative food (Folkvord, 1991; Hecht and Pienaar, 1993; Katavic *et al.*, 1989; Li and Mathias, 1982). Modeling studies have shown that smaller individuals are particularly vulnerable to reduction in prey availability (Post, 1990). Due to their reduced growth rate and metabolism, larger individuals are more resistant to starvation (Folkvord, 1991; Post, 1990). In addition, the larger individual generally have more food available owing to their wider range of acceptable prey sizes (Hunter and Kimbrell, 1980; Shirota, 1970).

A deductive inference based on the general knowledge about the ocean environment and the information of marine fish life history would lead to the possibility of cannibalism evolution of pelagic fish in larval stage. We are convinced that food requirement is not easily satisfied and mass reduction would occur by starvation in early life stage of pelagic fishes. In fish, predation is generally a size-selective process, usually limited by the mouth size of the predator (Folkvord, 1997; Otterå and Folkvord, 1993; Parazo *et al.*, 1991, Shirota, 1970, 1978; Sogard and Olla, 1994). Particularly, small larvae are limited potential available prey types.

The cannibalistic larval morphs typically have enlarged dentition and mouth dimensions and increased jaw musculature (Folkvord, 1997). In aquaculture, sea reaching and even in natural condition, it has been known that larva of some species having large mouth gape performs cannibalistic behavior (Bry *et al.*, 1992; Folkvord *et al.*, 1994; Hunter and Kimbrell, 1980; Otterå and Folkvord, 1993, Young and Davis, 1990).

Thus, there are several sound ecological and evolutionary reasons for cannibalism being a part of the natural behavioral repertoire of some fish species (Elger and Crespi, 1992; Polis, 1981). Therefore, although, how cannibalism commonly spreads in various fish species is not known, some ichthyologists believe that it is certainly likely to be more widespread in fish species (Dominey and Blumer, 1984; Folkvord, 1997; Smith and Reay, 1991).

In this paper we address possibility of intra-cohort cannibalism evolution in early life stage of marine pelagic fishes. We consider that the feature of location of spawning site (high sea or coastal/offshore) would cause larval cannibalism evolution. Unfortunately, we cannot directly test any hypotheses about cannibalism evolution in larvae of pelagic fishes at this time due to a lack of rich information. We hypothesize that mouth gape size of larvae would be enhanced to handle conspecific intra-cohort victims, if cannibalism occurs in the larval period. Large mouth gape also for other prey types that the size of these preys is as large as the larvae. However, we can suppose that the potential prey as large as the size of the larvae is very few excepts for the intra-cohort individuals in oligotrophic ocean environment. Thus, we consider the mouth gape morphology as a feature of cannibalism trait even if it play for the other potential prey.

We first compare larval morphology of the external feeding apparatus of the order Periciformes, that forms huge group of pelagic fishes, considering adult food habits and larval habitat types. We analyze how large mouth gape character would distribute within pelagic group of the order Periciformes. Next we construct a mathematical model to analyze evolutionary conditions of larval cannibalism according to habitat types and foraging efficiency to the conspecific intra-cohort victims, that would be related to mouth gape size.

The ecological features of pelagic fish

The notable feature of reproduction style of most marine fishes, especially compared to the terrestrial vertebrates, is that most of them scatter planktonic small eggs (1.203 ± 0.549 (SD) mm ($n = 180$ species) in diameter (Ochiai and Tanaka, 1986; Okiyama and Ueyanagi, 1977; Pepin, 1991; Shirota, 1978)) in large numbers. The egg-scattering reproductive style must have been the ancestral form of aquatic fauna and has apparently remained the suitable style for the dominant marine environment. The development of the eggs and larvae proceeds while drifting in the ocean currents. Yolk-sac larvae rely exclusively on endogenous nutrition from yolk of the ovum. The embryos have no active locomotor organ. After yolk absorption, sensory and locomotor organs are formed with development of digestive organs, and the larvae change from endogenous nutrition to exogenous feeding. The larvae of several pelagic fishes at the time of commencement of feeding is small and largely planktonic (4.57 ± 1.38 (SD) mm ($n = 28$ species) in length (Shirota, 1970)).

Spawning grounds of various high sea pelagic fish species are located in edge of the ocean and offshore regions where primary productivity is high relative to the mid ocean. Spawning design fits the prevailing currents, which are relied upon to bring the largely planktonic larvae to the nursery grounds. Typically, spawning grounds are 'upstream' in relation to ocean current flow from nursery grounds (Parrish *et al.*, 1981). On the way from the spawning grounds to the nursery grounds, reductions in the number of vulnerable larvae is caused by predation and starvation (Pepin, 1991).

Prey acquisition ability would be important to avoid starvation for the early stage larvae. Prey acquisition reflects the abundance of food particles of appropriate size relative to the larval feeding apparatus. Even in piscivorous species, larvae need small particles as food according to body size limitation. The ratio of larvae body size (or more directly, mouth gape size) and prey size is often considered as an important determinant of predation in aquatic systems (Johnson and Post, 1996; Shirota, 1970; Werner and Gilliam, 1984). Upon commencement of feeding, larvae usually have to rely on small planktonic particles, such as dinoflagellates, diatoms, tintinnids and nauplius of copepods due to the limitation of mouth size (Fortier and Villeneuve, 1995).

High seas oceanic regions, particularly in temperate and tropical region, where several adult piscivorous pelagic fishes occur, is generally known to have lower primary productivity than coastal and offshore regions. Reproductive strategies of pelagic fishes would be adapted to the oceanographic feature. For high seas migratory fishes such as marlins and tunas that have spawning and nursery grounds in tropical oligotrophic ocean edges where prey as well as predator are scarce, the abundance of small plankton and alternative prey would not be sufficient to avoid starvation for small larvae.

We hypothesized that the most common potential enough food source is the intra-cohort individuals, and if cannibalism occurs in the larval period, mouth gape size of larvae would be enhanced to handle conspecific intra-cohort victims. We analyzed how larval large mouth gape character would distribute within a taxonomic group considering phylogeny, adult food habits and larval habitat types. Our principal hypothesis was that larval cannibalism would evolve in oligotrophic high sea spawning and nursery grounds with large mouth gape size.

Morphological analyses

The order Periciformes is the most diversified of all fish orders, and their habitat spreads over almost all ocean environments (Nelson, 1984). Feeding mode ranges from planktonivorous to piscivorous. All pelagic forms of Periciformes spawn small plancktonic eggs, and their larvae experience the pelagic environmental condition mentioned above. We selected pelagic forms from two large suborders, Scombroidei and Percoidei, of the order Periciformes and analyzed how larval large mouth gape character distributes within the suborders. Okiyama (1988) was used as the main data source of larval morphology. We measured the relative upper jaw length to the body length for the specimen's illustration of each species and used as a data (% of upper jaw length) of the species. Only the illustrations of early larvae (length from 5 to 7 mm) were used. Information about adult food habits and larval habitats were obtained mainly from Ochiai (1986) and Okiyama (1988).

The suborder Scombroidei includes pelagic forms that inhabit and spawn in both high sea and offshore/coastal regions, and all species' adult food habit is piscivorous. On the other hand, the suborder Percoidei does not include high sea pelagic forms, but it includes species of both piscivorous and omnivorous adult food habit.

The morphological analysis of early larvae of pelagic fish species is not easy. The first difficulty is to collect specimens of early stage larvae. Even if we get specimens of a species, it is difficult to know the general information about the spawning site of the species. Even though we used a broad range of lower taxonomic groups in the analysis of the suborder Scombridei, we did not have sufficient information about spawning sites in some species. Particularly, the family Gempylidae (snake mackerels) is perplexing. There are few descriptions of life history about several species of the family. Based on some description (e.g. Okiyama, 1988), we categorize the species of the family as offshore/coastal spawners. Further, unfortunately, we could not collect large number of species' data in the analysis of the suborder Pericoidei. We found that only the genus Carangidae (jacks) includes piscivorors and omnivores. We listed all species that were used in the analyses in Appendix A.

We made a weak hypothesis that larval mouth gape size is larger in species of piscivorous adult food habit than in species of omnivorous adult food habit, using the data of the suborder Percoidei. This hypothesis tests the effect of factor, types of adult food habit given offshore/coastal dweller: whether an ontogenetic relationship of food habit in larva and in adult makes larval mouth gape size large to suit piscivors.

A strong hypothesis that larval mouth gape size is different between the species utilizing different spawning grounds, high sea and offshore/coastal, is tested using the data of the suborder Scombroidei. This hypothesis tests the effect of factor, types of habitat and spawning ground given that adult food habit is piscivorous: whether environment in larval stage makes larval mouth gape size large to suit cannibalism.

The latest established taxonomy lower than the suborder Scombroidei seems not to be monophyletic (Block *et al.*, 1993). We describe a molecular phylogenic tree of several genera of the suborder Scombroidei based on Block (1993). The phylogenic tree contains the most of genera and families of our data set (Fig. 1). Fig. 1 shows that (1) there exists no distinct pattern of habitat use among several genera and families, and (2) the conventional classification does not necessarily agrees with the phylogenic relation.

In our data set, the genus *Scomberomorus* includes species of high sea spawner (*Scomberomorus commerson*) and coastal spawner (*Scomberomorus niphonius*). The families Istiophoridae (billfishes) and Xiphiidae (swordfishes), are classified into the superfamily Xiphioidea, and the superfamily Xiphioidea is a distant group from the other groups of Scombridae (Block *et al.*, 1993; Nakamura and Parin, 1993).

Giving to these circumstances, we used means for each genera as independent measurements except for two instances. We calculated the mean value among species of the superfamily Xiphioidea, and used the mean as a single data point for species in the superfamily Xiphioidae. Since, the genus

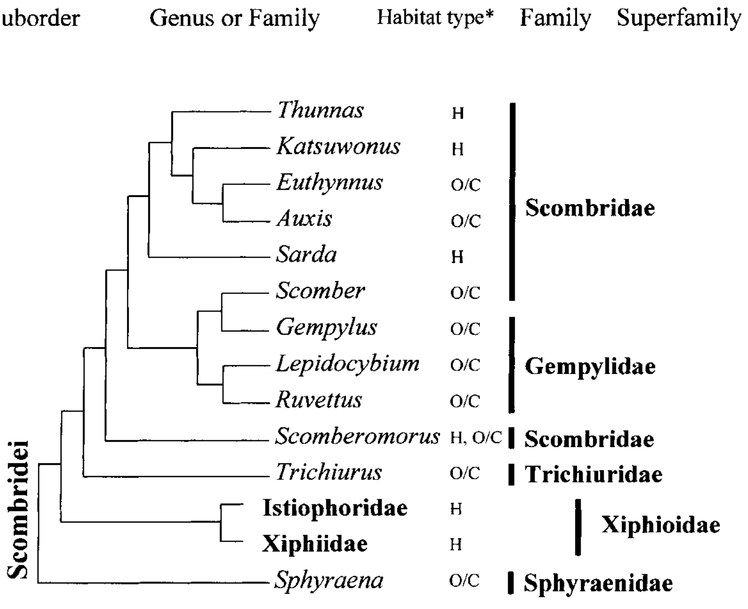


Figure 1. The phylogenic tree of the suborder Scombroidei based on the sequencing of a portion of the mitochondrial cytochrome *b* gene (rearranged after Block *et al.*, 1993). This diagram shows only the relative topological relationship of some genera and families of the suborder.
*Letter H in the column of habitat type expresses that it is known that the species in the higher taxa spawns in high sea ocean region. Letter O/C in the column of habitat type expresses that it is known that the species in the higher taxa spawns in coastal and offshore region.

Scomberomorus includes species which are both high sea spawners and offshore/coastal spawners, here, we used each species value for the analysis.

In the suborder Pericoidei, we found the family Carangidae (jacks) includes two classes of adult food habit, omnivore and piscivore. We used generic means as the data values in the data set of the family Carangidae.

Notice that we cannot unfortunately prepare a two (types of spawning site) by two (adult food habits) design analysis for a single taxonomic group to analyze the two hypotheses. The two hypotheses are tested independently by the two different taxonomic groups of the suborder Pericoidei.

We conducted a one-way ANOVA between two groups of Percoidei (omnivore vs. piscivore). There was no statistically significant difference between the groups ($F_{1,7} = 4.319$, $p < 0.0763$). Adult food habit has no effect on larval mouth gape size variation. The mean value of mouth gape size was 0.126% in the data set. Further, we conducted a one-way ANOVA between two groups of Scombroidei (high sea vs. offshore/coastal). There was statistically significant difference between the groups ($F_{1,22} = 39.200$, $p < 0.0001$). The mean mouth gape size of high sea spawners is larger than that of offshore/coastal spawners (0.295 and 0.153%, respectively).

Early larvae of the high sea migratory fish species, such as marlins and tunas, have larger mouth gapes than the fishes inhabiting offshore and coastal environments and the mouth size is close to a quarter of the body length. This morphological character would be adaptive to utilize large prey and enhance the breadth of prey types of the larvae. Although, it had been known that Scombroidei larvae of piscivores have large jaws (Okiyama and Ueyanagi, 1977), the functional role of the unique morphological character has not been ecologically understood. We built a model to explain why the high sea pelagic spawners have such large mouth gape in larval stage.

The mathematical model

Model structure

An oligotrophic ocean area in which eggs and larvae trasported on ocean current has poor fauna. Larvae of several millimeters in body length seldom meet ichthyoplankton that would be a potential good food source. Intra-cohort individuals would be only potential good prey except for several zooplankton species in the environment. Thus, cannibalism among intra-cohort larvae could be favored to evolve in larvae of pelagic fishes. Large mouth gape size relative to the body size would be an adaptive character for larvae handling prey as large as their body size. It can be stressed that intra-cohort individuals would be the most abundant large food source, and the potential good victims would be a selection force of larval feeding morphology.

To examine the evolutionary condition of early larva intra-cohort cannibalism in pelagic spawners, we constructed a simple model of population reduction and an individual's developmental growth processes during the larval period. We assume the following assumptions. Eggs are spawned in the upstream portion of a current. During the endogenous nutrition period, the larvae have no swimming ability and transported downstream by the current. After they have developed swimming and feeding organs, the larvae start exogenous feeding in the nursery area. The potential food menu is crustacea zooplankton and con-specific's ichthyolarvae. Predator and prey densities are modeled to increase from upstream to downstream of the current. The mortality factors considered were predation that was caused by predator species and intra-specific cannibals, and starvation. In the endogenous nutrition period larvae are subject to mortality only due to predation by hetero-specific predators. After commencement of exogenous feeding, utilizing not only hetero-specific potential prey but also con-specific intra-cohort individuals would reduce starvation risk and may accelerate the larval growth. However, spread of cannibalism behavior in the population leads a risk of predation by intra-cohort individuals.

The evolutionarily stable cannibalism rate is analyzed according to a high sea-coastal continuum of spawning sites under an assumption that cannibalism efficiency of intra-cohort individuals would reflect larval mouth gape size. We considered mouth gape size would reflect only the intake rate of con-specific victims, because we assumed that there is no potential prey sized as large as the con-specific individuals and effect of change of mouth gape size for intake rate of other planktonic preys is negligible.

A model to investigate evolution of cannibalism during early larval period in current flow can be derived as follows. Let n_{w} and n_{m} denote the numbers of survivors from a single clutch of common wild and rare mutant, B_{w} and B_{m} denote the larval body masses of the wild and the mutant, respectively. $n_{\mathrm{w}}(0)$ and $n_{\mathrm{m}}(0)$ are the numbers of eggs spawned by a wild and a mutant $(n_{\mathrm{w}}(0) = n_{\mathrm{m}}(0))$. $B_{\mathrm{w}}(0)$ and $B_{\mathrm{m}}(0)$ are egg masses of the both types $(B_{\mathrm{w}}(0) = B_{\mathrm{m}}(0))$.

N_{w} and N_{m} denote the numbers of wild type spawners and mutant spawners, respectively, and N denotes the total number of spawners. As is usual in ESS analysis, we assume that the mutant is very rare compared to the wild type $(N_{\mathrm{m}} = 1 \ll N_{\mathrm{w}} \approx N)$.

Assume that the larvae necessarily attack hetero-specific prey upon encounter, and attack con-specific individuals according to degree of cannibalism (cannibalism rate). The attack probabilities (cannibalism rates) upon encounter of wild and mutant are p_{w} and p_{m} respectively. When two encountering individuals perform cannibalistic behavior, either individual can eat the opponent with probability 0.5.

In a medium, particles would be made sparse from a source point (spawning place) by diffusion, and results in a Gaussian distribution. Even though it is not strictly true, for simplicity, we assume that there exists a single spawning point and diffusion of particles (larvae) in the current flow would maintain the distribution of larvae as a Gaussian. Encounters with con-specific larvae occur in a current flow with the diffusion process. Let $G(r,t) = \left(1/\sqrt{4\pi Dt}\right)\mathrm{e}^{-r^2/(4Dt)}$ which is a Gaissian probability density of larvae at place r from the center of the distribution at time t, where D is diffusion constant. The total number of wild type larvae and the total number of mutant larvae at place r from the center of the distribution at time t are $N_{\mathrm{w}}(r,t) = Nn_{\mathrm{w}}(t)G(r,t)$ and $N_{\mathrm{m}}(r,t) = n_{\mathrm{m}}(t)G(r,t)$, respectively. The expected number of encounters between larvae of a wilde or a mutant clutch and larvae of the other clutches in small time interval δt can be written approximately as

$$\left[\oint_r N_{\mathrm{w}}(r,t)\frac{N_{\mathrm{w}}(r,t)}{N}\mathrm{d}r\right]\delta t \propto \left(\frac{dNn_{\mathrm{w}}}{\sqrt{t}}\right) n_{\mathrm{w}}\delta t \tag{1}$$

and

$$\left[\oint_r N_{\mathrm{w}}(r,t)N_{\mathrm{m}}(r,t)\mathrm{d}r\right]\delta t \propto \left(\frac{dNn_{\mathrm{w}}}{\sqrt{t}}\right)n_{\mathrm{m}}\delta t, \tag{2}$$

where d is a positive constant (Appendix B). $\left(dNn_{\mathrm{w}}/\sqrt{t}\right) = \varsigma(N, n_{\mathrm{w}})$ is a per capita instantaneous encounter rate of intra-cohort individuals at time t.

The dynamics of number of survivors in cohorts and the dynamics of individual's growth of larvae in exogenous larval period are described by the following basic equations;

$$\frac{\mathrm{d}n_{\mathrm{w}}}{\mathrm{d}t} = -\left[\frac{1}{B_{\mathrm{w}}}\left(\mu(x) + \frac{c}{\lambda(x) + 0.5(1-(1-p_{\mathrm{w}})^2)\varsigma(N,n_{\mathrm{w}})}\right)\right.$$
$$\left. +\ 0.5(1-(1-p_{\mathrm{w}})^2)\varsigma(N,n_{\mathrm{w}})\right]n_{\mathrm{w}} \tag{3}$$

$$\frac{\mathrm{d}n_{\mathrm{m}}}{\mathrm{d}t} = -\left[\frac{1}{B_{\mathrm{m}}}\left(\mu(x) + \frac{c}{\lambda(x) + (0.5p_{\mathrm{m}}p_{\mathrm{w}} + p_{\mathrm{m}}(1-p_{\mathrm{w}}))\varsigma(N,n_{\mathrm{w}})}\right)\right.$$
$$\left. +\ (0.5p_{\mathrm{m}}p_{\mathrm{w}} + p_{\mathrm{w}}(1-p_{\mathrm{m}}))\varsigma(N,n_{\mathrm{w}})\right]n_{\mathrm{m}} \tag{4}$$

$$\frac{\mathrm{d}B_{\mathrm{w}}}{\mathrm{d}t} = g\left[\frac{\lambda(x)e_1 + 0.5(1-(1-p_{\mathrm{w}})^2)\varsigma(N,n_{\mathrm{w}})e_2}{1 + \lambda(x)h_1 + 0.5(1-(1-p_{\mathrm{w}})^2)\varsigma(N,n_{\mathrm{w}})h_2}\right]B_{\mathrm{w}} \tag{5}$$

$$\frac{\mathrm{d}B_{\mathrm{m}}}{\mathrm{d}t} = g\left[\frac{\lambda(x)e_1 + (0.5p_{\mathrm{m}}p_{\mathrm{w}} + p_{\mathrm{m}}(1-p_{\mathrm{w}}))\varsigma(N,n_{\mathrm{w}})e_2}{1 + \lambda(x)h_1 + (0.5p_{\mathrm{m}}p_{\mathrm{w}} + p_{\mathrm{m}}(1-p_{\mathrm{w}}))\varsigma(N,n_{\mathrm{w}})h_2}\right]B_{\mathrm{m}} \tag{6}$$

where $\mu(x)$ and $\lambda(x)$ are instantaneous encounter rates of hetero-specific predator and prey on given place x on the current flow, respectively ($\mu(x) \propto \lambda(x)$), e_1 and e_2 are net energies, and h_1 and h_2 are handling times, of hetero-specific preys and intra-cohort victims, respectively. c is a positive constant. Both $\mu(x)$ and $\lambda(x)$ are monotonically increasing function of x. We assume that $\mu(x) = a\mathrm{e}^{sx}$ and $\lambda(x) = b\mathrm{e}^{sx}$, respectively, where a, b and s are positive constants.

We assume that the instantaneous death rates due to predation by hetero-specific predators and starvation are reciprocally proportional to the larval body size. The higher predation by other predator species is modeled by higher values of $\mu(x)$. Death by starvation is assumed proportional with respect to the expected waiting time of successive attacks of prey. Assuming that the encounters occur by Poisson processes, the expected waiting time of attacking a prey is reciprocally proportional to the sum of the instantaneous rates of successful attack to hetero-specific and con-specific prey individuals.

The first terms in the brackets of Equations (3) and (4) express the instantaneous death rate due to predation by hetero-specific predators and starvation for wild and mutant individuals, respectively. The second terms in the brackets of Equations (3) and (4) express the instantaneous death rate due to intra-cohort cannibalism. In this process we assumed that handling times (h_1 and h_2) are vanishingly smaller than waiting time of encounter to either prey types, con-specific and hetero-specific. The fractions in Equations (5) and (6) express the instantaneous energy intake rates (Stephens and Krebs, 1986). We assume that the growth of body mass of individual larva is proportional to the instantaneous rate of energy gain and the body mass. Number of surviving larvae in a cohort and the larval body mass can be considered as functions of the cannibalism rate of wild p_{w} and mutant p_{m} under the given conditions.

We assume that growth does not start and body mass is kept as $B(0)$, and number of survivers decreases only due to predation by hetero-specific predators during the endogenous period. The spawning ground locates at $x_0 = 0$. The planktonic endogenous larvae are transported and reach the nursery ground at time $\tilde{t}$. The larvae reaching the nursery ground stay there during a certain period of the juvenile stage, $T - \tilde{t}$, and conduct exogenous feeding. We assume that $\tilde{t} \propto B(0)$ because that the yolk absorption period is positively correlated to the egg volume (Miller *et al.*, 1988). Thus, the nursery ground is located on $x = x_0 + v\tilde{t}$, where v is the current velocity.

Predator and prey density gradients from the spawning to nursery grounds in high sea, offshore and coastal areas were expressed by multiplying a positive factor, α, to $\mu(x)$ and $\lambda(x)$. Small α values indicate a high sea oligotrophic spawning and nursery environment and large α value indicates coastal eutrophic ones. We assume that large mouth gape is adapted to increase handling ability of prey upon encounter, particularly to potential good prey (con-specific victims). We designate β as an indicator of mouth gape size and foraging efficiency of con-specific intra-cohort individuals (e_2/h_2). Large mouth gape size will increase the profitability of con-specific victims rather than of crustacea zooplankton. Larvae having large mouth gape have large β value. For simplicity, β is invariant through the developing period. We evaluate evolutionarily stable cannibalistic rates along the parameter space of α and β. We set a conservative assumption to favor cannibalism evolution: the profitability of con-specific victim is lower than that of hetero-specific prey, $e_2/h_2 = \beta < e_1/h_1$.

The fitness of each wild or mutant type, W_{w} or W_{m}, can be defined as the product of the proportion of survivers $(n(t)/n(0))$ and the expected body mass of larva $(B(t))$ at time $t = T$, that is: $W_{\mathrm{w}}(p_{\mathrm{w}}, p_{\mathrm{w}}) = n_{\mathrm{w}}(T, p_{\mathrm{w}}, p_{\mathrm{w}})/n_{\mathrm{w}}(0) B_{\mathrm{w}}(T, p_{\mathrm{w}}, p_{\mathrm{w}})$, $W_{\mathrm{m}}\ (p_{\mathrm{m}}, p_{\mathrm{w}}) = n_{\mathrm{m}}(T, p_{\mathrm{m}}, p_{\mathrm{w}})/n_{\mathrm{m}}(0) B_{\mathrm{m}}(T, p_{\mathrm{m}}, p_{\mathrm{w}})$, respectively. If $W_{\mathrm{m}}(p_{\mathrm{m}}, p_{\mathrm{w}}) < W_{\mathrm{w}}\ (p_{\mathrm{w}}, p_{\mathrm{w}})$ holds, the population that consists of individuals of p_{w} cannibalistic rate is stable against invasion of mutant having p_{m} cannibalistic rate, and vice versa.

We conducted numerical analysis given the parameter values; $a = 0.025$, $b = 0.125$, $c = 0.1$, $d = 1 \times 10^{-7}$, $g = 2$, $s = 2$, $e_1 = 1$, $h_1 = 1$, $N_w = 1 \times 10^7$, $N_m = 1$, $n_w(0) = 1$, $n_m(0) = 1$, $v = 1$, $B(0) = 1$, and $T = 10$.

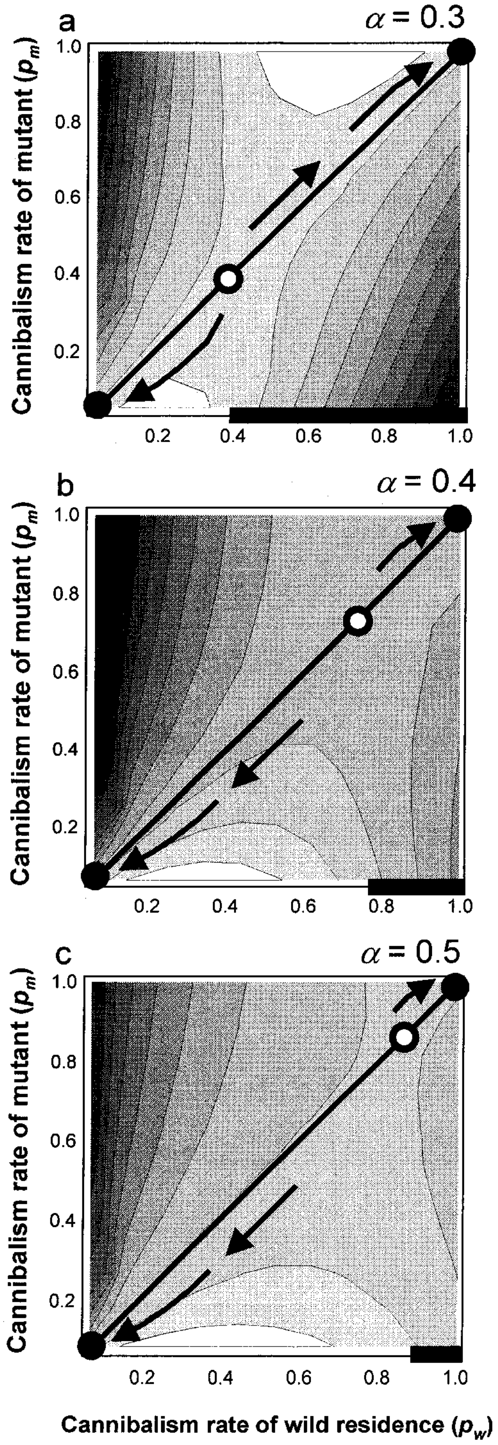
Results of the model

We have done a pairwise global invasibility analysis (Kisdi and Meszena, 1993) to evalulate the evolutionary dynamics of cannibalism rate. For every combination of cannibalism rates of wild p_w and mutant p_m, the logarithm of the fitness ratio $(\ln(W_m(p_m, p_w)/W_w(p_w, p_w)))$ has been calculated numerically to find out who can invade against what types of wild population, and hence find all the ESSs (see details in Kisdi (1993)).

Fig. 2 showed the invasibility maps of three different parameter values of high sea and offshore/coastal gradient α. Both $p_w = 0$ and $p_w = 1$ would be possible ESS cannibalism rates. Attainability of each ESS depends on initial condition of cannibalism rate in the population, that is, there exists a threshold value which is a bifurcation point of evolutionary dynamics. When an initial wild population had cannibalism rates lower than the bifurcation point, a mutant having lower cannibalism rate than that of the wild type can invade. Consequently, no cannibalism would evolve and the character will be table. On the contrary, when an initial population had cannibalism rate higher than the bifurcation point, a mutant having higher cannibalism rate than that of the wild type can invade. Complete cannibalism would evolve and the character will be stable.

Environmental factors as characterized by high sea and coastal/offshore gradient affects attainable cannibalism rate and stability of the cannibalism rate in evolutionary dynamics. The bifurcation point would shift to lower value of cannibalism rate in a high sea environment (i.e. small α value, see Fig. 2a, $\alpha = 0.3$), and the wide range of initial cannibalism rate higher than the bifurcation point would make population into complete cannibalism ($p_w = 1$). On the contrary, the bifurcation point would shift toward higher value of cannibalism rate in coastal/offshore environment (i.e. large α value, see Fig. 2c, $\alpha = 0.5$), and the wide range of initial cannibalism rate lower than the bifurcation point would make population into complete non-cannibalism ($p_w = 0$).

In an extreme case of small α, any population consisting of individuals having cannibalism rates less than one is invaded by mutants having cannibalism rates higher than that of the wild type, due to shift of the bifurcation point less than 0. Consequently complete cannibalism ($p_w = 1$) would evolve and the character will be stable against invasion of any mutant. In an alternative extreme case (large α), any population consisting of individuals having cannibalism rates greater than 0 is invaded by mutants having cannibalism rates lower than that of the wild type, due to shift of the bifurcation point beyond 1. No cannibalism ($p_w = 0$) would evolve and the character will be stable.


a
α = 0.3
b
α = 0.4
c
α = 0.5
Cannibalism rate of mutant (p_m)
1.0
0.8
0.6
0.4
0.2
0.2
0.4
0.6
0.8
1.0
Cannibalism rate of wild residence (p_w)

◄

Figure 2. Invasibility maps. Relative fitness of invading cannibalism strategy as a function of its own strategy (ordinate) and the strategy of the resident (abscissa) for different parameters (the logarithm of the fitness ratio $(\ln(W_{\mathrm{m}}(p_{\mathrm{m}},p_{\mathrm{w}})/W_{\mathrm{w}}(p_{\mathrm{w}},p_{\mathrm{w}})))$. The logarithm of relative fitness of invader is equal to zero along the diagonal line (i.e. the mutant is identical to the wild type). Contour lines of invader's fitness are shown. Fitness value becomes low from light to dark. Parameter value of cannibalism efficiency is $\beta = 0.1$. Figures from (a) to (c) correspond to form high sea to coastal environment. Arrows shows transient and convergence behavior of evolutionary dynamics. Solid circles show ESSs, and open circle shows the bifurcation point of evolutionary dynamics (see text). The bold lines in the horizontal axes indicate the range of initial cannibalism rate leading to ESS state of complete cannibalism.

Acquisition efficiency of a con-specific victim, β, which reflects mouth gape size, would also affect cannibalism evolution. High acquisition efficiency of con-specific victim might make it more likely to evolve cannibalism. Fig. 3 showed the change of bifurcation point with respect to the environmental gradient (i.e. parameter α) and the prey acquisition efficiency parameters (i.e. parameter β). The bifurcation point becomes low as acquisition efficiency of con-specific victim increases in each environment. The higher the cannibalism efficiency (large value β) and the lower the environmental productivity (small value of α), the higher the possibility of stabilization of cannibalism.

Discussion

We found that a deductive inference based on the general knowledge about the ocean environment and the information of marine fish life history would lead possibility of cannibalism evolution of pelagic fish larvae.

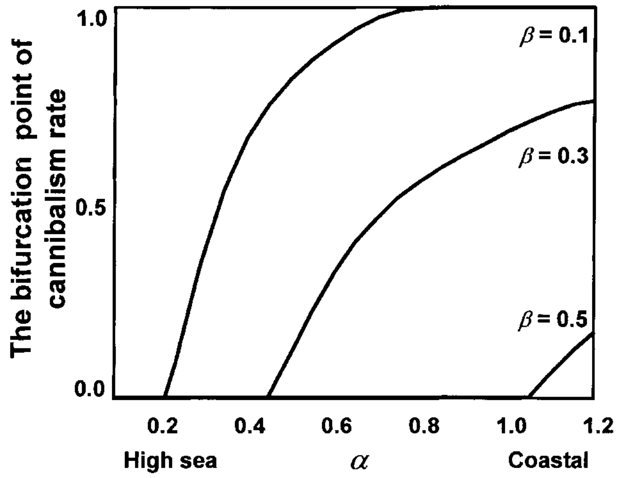


Figure 3. Change of bifurcation point with respect to environmental gradient (α) and cannibalism efficiency (β). See details in the text.

Cannibalism can be considered as foraging problem in low food environments. Dong and Polis (1992) argued that oligotrophic environment and/or high acquisition efficiency of con-specific victim would support the evolution of cannibalism character and vice versa. Additional factors should be considered to argue possibility of cannibalism evolution in pelagic fish larvae. Since we assumed that cannibalism occurs among intra-cohort individuals, a cannibal would also be a potential victim of the other cannibals. If a cannibalistic character occurs in a population, it could have two opposite effects on individual fitness. (1) Mortality caused by predation would increase because that con-specific individuals take part in predation. (2) On the other hand, mortality caused by starvation would be decreased due to increments in encounter rate of potential prey by including con-specific individuals as prey item. This would have positive effect on the evolution of cannibalism even if the con-specific victim's profitability as prey is low. Therefore, cannibalism evolution is not only a foraging problem but also a game theory one. Thus, since diffident individuals suffer unilateral predation threats from cannibalistic individuals, even where cannibalism is not profitable according to foraging theory, there is a possibility to evolve cannibalism.

Gradients of primary productivity from offshore/coastal to high sea environment change the balance of the positive and the negative pressure for cannibalism evolution. We are convinced that the food requirement is not easily satisfied and mass mortality would occur by starvation in early life stage of pelagic fishes, particularly in a high sea environment. Reduction of starvation risk should be selected for during pelagic life in the early larval stage. Since cannibalism reduces starvation risk, if a large mouth gape size in larvae of high sea pelagic fishes promotes feeding efficiency of fish larvae, cannibalism tends to evolve and the character should be successfully stabilized in their history.

We adopted a conservative assumption about profitability of con-specific victims to expect evolution of cannibalism in our model analysis (i.e. profitability of con-specifics is lower than that of hetero-specifics). But, since the proximal composition of the prey is similar to the proximal composition of the cannibal, there are some indications that cod and other fishes and amphibians grow better on a diet of con-specifics (Crump, 1992; Folkvord and Otterå, 1993). This suggests that the evolution of cannibalism may be more likely than we suggest.

We premised that intra-cohort cannibalism necessarily requires large mouth gape. Actually, intra-cohort cannibalism is mouth-size limited. Around metamorphosis, larval cod (*Gadus morhua*) has relatively large mouth and starts cannibalism (Otterå and Folkvord, 1993). In flatfish, the increased body height of post metamorphosis is not accompanied by a corresponding increase in mouth gape, thus reducing the possibility of coeval cannibalism (Folkvord, 1997). There are some other observations that mouth size of the cannibal relative to the size of the victim limits the success of cannibalism (Parazo *et al.*, 1991; Sogard and Olla, 1994). Our premise is justified by these observations.

Our mathematical model suggests that in an extreme case (in oligotrophic environments) cannibalism is necessarily attainable and stable, and in another extreme case (in coastal environment) non-cannibalism is necessarily attainable and stable. Generally the model has two possible ESS states (cannibalism and non-cannibalism). Feasibility of either ESS generally depends on the initial condition of cannibalism rate in the population, location on the environmental gradient (high sea to coastal/offshore), and cannibalism efficiency that might be related to mouth gape size. This means that, even if a group of a phylogenetic lineage shared an ancestor having some degree of cannibalism rate around the bifurcation point on Fig. 2 ($0 < p < 1$) and thus in the past shared similar morphology, the monophyletic species do not necessarily belong to same category of cannibalism rate. Some taxon would evolve to non-cannibal states and the others would evolve to cannibals depending on how the evolutionary pass ways walked around the bifurcation point of cannibalism rate. This inference suggests that cannibalistic and non-cannibalistic species would coexist in an intermediate range of the ocean environment, and cannibalism is dominated in high sea environment.

Some of the predictions of our model are not literally meaningful. Our prediction of ESS cannibalism rates of $p = 1$ or $p = 0$, were done to simplify the model's structure. More complex models incorporating state dependence of cannibalism rate would produce more realistic predictions, however, our model presents qualitatively useful prediction for cannibalism evolution in pelagic fish larvae.

Our morphological analysis suggested that large mouth gape distributes in the group of Scombroidei that inhabit in high sea environment. Unfortunately, information about early stage intra-cohort cannibalism of pelagic fish species is insufficient to verify our predictions (Smith and Reay, 1991). There is a possibility to detect cannibalism in pelagic larvae, but rapid digestion of smaller con-specific prey will require large numbers of potential predators to be investigated. Cannibalism in juveniles has been reported in a few pelagic fish species in natural condition (Bogstad *et al.*, 1994; Koeller *et al.*, 1989; Perry and Neilson, 1988; Young and Davis, 1990). However, Young and Davies (1990) observed intra-cohort cannibalism in 1.5% of the southern bluefin tuna, *Thunnus maccoyii*, larvae with food in their stomachs. The consumed larvae were smaller than 4 mm, and occurred in 3 out of 16 (19%) of the larvae between 8 and 9.5 mm length.

The deductive implication of the model predictions provides rich idea to understand the fragmented knowledge of pelagic fish life history. Our formal mathematical analysis and the morphological analysis shed light on evolutionary conditions favoring cannibalism in early larval stages of pelagic fishes, and provide an explanation of large mouth gape of several larvae of high sea pelagic spawners.

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Appendix A

Species used to the morphological analysis

Suborder		Scombroidei	
Adult food habit		Piscivorous	
Spawning and nursery grounds	Offshore/Coastal		High sea
Scombridae		Istiophoridae	
	Scomber japonicus		*Tetrapturus audax*
	S. australasicus		*T. angustirostris*
	Scomberomorus niphonius		*Istiophorus platypterus*
	Auxis rohei		*Makaira mazara*
	Euthynnus affinis		*M. indica*
	Grammatorcynus bilineatus	Xiphiidae	
			Xiphias gladius
Gempylidae		Scombridae	
	Gempylus serpens		*Thunnus albacares*
	Neoepinnula orientalis		*T. obesus*
	Pexea prometheoides		*T. alalunga*
	Nealotus tripes		*T. thynnus*
	Ruvettus pretiosus		*T. maccoyii*
	Promethichthys prometheus		*Katsuwonus pelamis*
	Lepidocybium flavobrunneum		*Scomberomorus commerson*
	Nesiarchus nasutus		
	Diplospinus multistiriatus		*Acanthocybium solandri*
			Gtmnosarda unicolor
			Sarda orientalis
Trichiuridae			
	Trichiurus lepturus		
	Benthodesmus elongatus		
	Eupleurogrammus muticus		
Sphyraenidae			
	Sphyraena barracuda		
	S. pinguis		
	S. japonica		

Appendix A (Continued)

Suborder		Pericoidei	
Family		Carangidae	
Adult food habit	Piscivorous		Omnivorous
Spawning and nursery grounds		Offshore/Coastal	
	Seriola quinqueradiata *S. lalandi* *S. dumerili* *Scomberoides lysan* *Naucrates ductor* *Elagatis bipinnulata* *Seriolina nigrofasciata*		*Trachurus japonicus* *Decapterus muroadsi* *D. macarellus* *D. macrosoma* *D. maruadi* *Pseudocaranx dentex* *Selar crumenophthalmus*

Appendix B

Substitute $N_{\mathrm{w}}(r,t) = Nn_{\mathrm{w}}(t)G(r,t)$ into $\left[\oint_r N_{\mathrm{w}}(r,t)N_{\mathrm{w}}(r,t)/N\mathrm{d}r\right]\delta t$ and rearrange it as follows;

$$\begin{aligned}\left[\oint_r N_{\mathrm{w}}(r,t)\frac{N_{\mathrm{w}}(r,t)}{N}\mathrm{d}r\right]\delta t &= \left[Nn_{\mathrm{w}}^2(t)\oint_r G^2(r,t)\mathrm{d}r\right]\delta t\\ &= \left[Nn_{\mathrm{w}}^2(t)\oint_r \left(\frac{1}{\sqrt{4\pi Dt}}\mathrm{e}^{-r^2/(4Dt)}\right)^2\mathrm{d}r\right]\delta t\\ &= \left[\frac{Nn_{\mathrm{w}}^2(t)}{\sqrt{8\pi Dt}}\oint_r \frac{1}{\sqrt{2\pi Dt}}\mathrm{e}^{-r^2/(2Dt)}\mathrm{d}t\right]\delta t\\ &= \left[\frac{Nn_{\mathrm{w}}^2(t)}{\sqrt{8\pi Dt}}\right]\delta t \propto \left(\frac{dNn_{\mathrm{w}}}{\sqrt{t}}\right)n_{\mathrm{w}}\delta t,\end{aligned}$$

where $d = 1/\sqrt{8\pi D}$. Similarly, substitute $N_{\mathrm{w}}(r,t) = Nn_{\mathrm{w}}(t)G(r,t)$ and $N_{\mathrm{m}}(r,t) = n_{\mathrm{m}}(t)G(r,t)$ into $\left[\oint_r N_{\mathrm{w}}(r,t)N_{\mathrm{m}}(r,t)\mathrm{d}r\right]\delta t$ and rearrange it as follows;

$$\begin{aligned}\left[\oint_r N_{\mathrm{w}}(r,t)N_{\mathrm{m}}(r,t)\mathrm{d}r\right]\delta t &= \left[Nn_{\mathrm{w}}(t)n_{\mathrm{m}}(t)\oint_r G^2(r,t)\mathrm{d}r\right]\delta t\\ &= \left[Nn_{\mathrm{w}}(t)n_{\mathrm{m}}(t)\oint_r \left(\frac{1}{\sqrt{4\pi Dt}}\mathrm{e}^{-r^2/(4Dt)}\right)^2\mathrm{d}r\right]\delta t\\ &= \left[\frac{Nn_{\mathrm{w}}(t)n_{\mathrm{m}}(t)}{\sqrt{8\pi Dt}}\right]\delta t \propto \left(\frac{dNn_{\mathrm{w}}}{\sqrt{t}}\right)n_{\mathrm{m}}\delta t,\end{aligned}$$

where $d = 1/\sqrt{8\pi D}$.

References

Block, B.A., Finnerty, J.R., Stewart, A.F.R. and Kidd, J. (1993) Evolution of endothermy in fish: mapping physiological traits on a molecular phylogeny. *Science* **260**, 210–214.

Bogstad, B., Lilly, G., Mehl, S., Pálsson, Ó.K. and Stefánsson, G. (1994) Cannibalism and year-class strength in Atlantic cod (*Gadus morhua* L.) in the Arcot-boreal ecosystems (Barents Sea, Iceland and Eastern Newfoundland). *ICES Marine Sci. Sympo*. **198**, 576–599.

Bry, C., Basset, E., Rognon, X. and Bonamy, F. (1992) Analysis of sibling cannibalism among pike, *Esox lucius*, juveniles reared under semi-natural conditions. *Envi. Biol. Fish*. **35**, 75–84.

Crump, M.L. (1992) Cannibalism in amphibians. In: M.A. Elgar and B.J. Crespi (eds) *Cannibalism: Ecology and Evolution among Diverse Taxa*. Oxford University Press, Oxford, pp. 256–276.

DeAngelis, D.L., Cox, D.K. and Coutant, C.C. (1979) Cannibalism and size dispersal in young-of-the-year largemouth bass: experiment and model. *Ecol. Model*. **8**, 133–148.

Dominey, W.J. and Blumer, L.S. (1984) Cannibalism of early life stages in fishes. In G. Hausfater and S.B. Hrdy (eds) *Infanticide, Comparative and Evolutionary Perspective*. Aldine, New York, pp. 43–64.

Dong, Q. and Polis, G.A. (1992) The dynamics of cannibalistic populations: a foraging perspective. In: M.A. Elger and B.J. Trespi (eds) *Cannibalism*. Oxford University Press, Oxford, pp. 13–37.

Elger, M.A. and Crespi, B.J. (1992) Ecology and evolution of cannibalism. In M.A. Elger and B.J. Crespi (eds) *Cannibalism*. Oxford University Press, Oxford, pp. 1–12.

Folkvord, A. (1991) Growth, survival and cannibalism of cod juveniles (*Gadus morhua* L.): effects of feed type, starvation and fish size. *Aquaclture* **97**, 41–59.

Folkvord, A. (1997) Ontogeny of cannibalism in larval and juvenile fishes with special emphasis on Atlantic cod. In R.C. Chambers and E.A. Trippel (eds) *Early Life History and Recruitment in Fish Populations*. Chapman & Hall, London, pp. 251–278.

Folkvord, A. and Otterå, H. (1993) Effects on initial size distribution, day length and feeding frequency on growth, survival and cannibalism in juvenile Atlantic cod (*Gadus morhua* L.) *Aquaculture* **114**, 243–260.

Folkvord, A., Øiestad, V. and Kvenseth, P.G. (1994) Growth patterns of three cohorts of Atlantic cod larvae (*Gadus morhua* L.) studied in a macrocosm. *ICES Journal of Marine Sci*. **51**, 325–336.

Fortier, L. and Villeneuve, A. (1995) Cannibalism and predation on fish larvae by larvae of Atlantic mackerel, *Scomber scombrus*: trophodynamics and potential impact on recruitment. *Fish. Bull*. **92**, 268–280.

Fox, L.R. (1975) Cannibalism in natural populations. *Ann. Rev. Ecol. Syst*. **6**, 87–106.

Hecht, T. and Pienaar, A.G. (1993) A review of cannibalism and its implications in fish larviculture. *Journal of the World Aquacul. Soci*. **241**, 246–261.

Hunter, J.R. and Kimbrell, C.A. (1980) Early life history of Pacific mackerel, *Scomber japonicus*. *Fish. Bull., US*. **78**, 89–101.

Johnson, J.M. and Post, D.M. (1996) Morphological constraints on intracohort cannibalism in age-0 Largemouth bass. *Trans. Am. fish. Soci*. **125**, 809–812.

Katavic, I., Jug-Dujakovic, J. and Glamuzina, B. (1989) Cannibalism as a factor affecting the survival of intensively cultured sea bass (*Dicentrarchus labrox*) fingerlings. *Aquaculture* **77**, 135–143.

Kisdi, E. and Meszena, G. (1993) Density dependent life history evolution in fluctuating environments. In J. Yoshimura and C.W. Clark (eds) *Adaptation in Stochastic Environments* Springer-Verlag, Berlin, pp. 26–62.

Koeller, P.A., Coates-Markle, L. and Neilson, J.D. (1989) Feeding ecology of juvenile (age-0) silver hake (*Merluccius bilinearis*) on the Scotian Shelf. *Cana. J. Fish. Aqua. Sci*. **46**, 1762–1768.

Li, S. and Mathias, J.A. (1982) Causes of high mortality among cultured larval walleyes. *Trans. Am. Fish. Soci*. **111**, 710–721.

Miller, T.J., Crowder, L.B., Rice, J.A. and Marschall, E.A. (1988) Larval size and recruitment mechanisms in fishes: toward a conseptual framework. *Cana. J. Fish. Aqua. Sci*. **45**, 1657–1670.

Nakamura, I. and Parin, N.V. (1993) FAO species catalogue. Vol 15. Snake mackerels and cutlassfishes of the world (Families Gempylidae and Trichiuridae). *FAO Fish. Synop*. **15**, 1–136.

Nelson, J.S. (1984) *Fishes of the world*, 2nd edn. John Wiley & Sons, New York.

Ochiai, A. and Tanaka, M. (1986) *Ichtyhology II.* Kouseisya, Tokyo, Japan.

Okiyama, M. and Ueyanagi, S. (1977) Larvae and juvenile of the Indo-Pacific dogtooth tuna, (Rüpell). *Bull. Far Seas Fish. Res. Lab. Jpn.* **15**, 35–49.

Okiyama, M. (1988) *An atlas of the early stage fishes in Japan.* Tokai University Press, Tokyo.

Otterå, H. and Folkvord, A. (1993) Allometric growth in juvenile cod (*Gadus morhua* L.) and possible effects on cannibalism. *J. Fish Biol.* **43**, 643–645.

Parazo, M.M., Avila, E.M. and Reyes, D.M.J. (1991) Size- and weight dependent cannibalism in hatchery-bred sea bass (*Lates calcarifer* Bloch). *J. Appl. Ichthyol.* **7**, 1–7.

Parrish, R.H., Nelson, C.S. and Bakun, A. (1981) Transport mechanisms and reproductive success of fishes in the California current. *Biol. Oceanog.* **1**, 175–203.

Pepin, P. (1991) Effect of temperature and size on development, mortality, and survival rates of the pelagic early life history stages of marine fish. *Cana. J. Fish. Aqua. Sci.* **48**, 503–518.

Perry, R.I. and Neilson, J.D. (1988) Vertical distributions and trophic interactions of age-0 Atlantic cod and haddock in mixed and stratified waters of Georges Bank. *Marine Ecol. Prog. Seri.* **49**, 199–214.

Polis, G.A. (1981) The evolution and dynamics of intraspecific predation. *Ann. Rev. Ecol. Syst.* **12**, 225–251.

Post, J.R. (1990) Metabolic allometry of larval and juvenile yellow parch (*Perca flavescens*): in situ estimates and bioenergetic models. *Cana. J. Fish. Aqua. Sci.* **47**, 554–560.

Ridley, M. (1996) *Evolution*, 2nd edn. Blackwell, Cambridge.

Shirota, A. (1970) Studies on the mouth size of fish larvae. *Bull. the Japanese Soci. Sci Fish* **36**, 353–368.

Shirota, A. (1978) Studies on the mouth size of fish larvae-II: specific characteristics of the upper jaw length. *Bull. the Japanese Soci. Sci Fish.* **44**, 1171–1177.

Smith, C. and Reay, P. (1991) Cannibalism in teleost fish. *Rev. Fish Biol. Fish.* **1**, 44–64.

Sogard, S. and Olla, B.L. (1994) The potential for intracohort cannibalism in age-0 walleye pollock, *Theragra chalcogramma* as determined under laboratory conditions. *Env. Biol. Fish.* **39**, 183–190.

Stenseth, N.C. and Reed, J. (1978) A comment on Bobisud's paper on evolution of cannibalism. *Bull. Math. Biol.* **40**, 541–545.

Stephens, D.W. and Krebs, J.R. (1986) *Foraging theory*. Princeton University Press, New Jersey.

Werner, E.E. and Gilliam, J.F. (1984) The ontogenic niche and species interactions in size-structured populations. *Ann. Rev. Ecol. Syst.* **15**, 393–425.

Young, J.W. and Davis, T.L.O. (1990) Feeding ecology of larvae of southern bluefin, albacore and skipjack tunas (Pisces: Scombridae) in the eastern Indian ocean. *Marine Ecol. Prog. Seri.* **61**, 18–29.