

Abstract.—The sandfish family Trichodontidae is comprised of two species endemic to the boreal Pacific: *Arctoscopus japonicus* is a common demersal fish of commercial importance in the western area around northern Japan, while *Trichodon trichodon* is found in the eastern waters, from Alaska to California, although there is no fishery for this species. The two species share many similar reproductive features such as large demersal eggs of 3.3–3.5 mm diameter, moderate fecundities of 1000–2000 eggs, and peculiar spawning habits on rocky shores. However, there are striking contrasts in several reproductive and early-life-history traits: the shape of the egg mass is spherical in *A. japonicus* versus an irregular shape in *T. trichodon*; spawning substrate is mostly *Sargassum* spp. versus rock; incubation period is about 2 months versus nearly 1 year; and, at hatching, *T. trichodon* has precocious pectoral and caudal rays as well as preopercular spines. Despite these differences, larvae of both species appear in the spring season. These features are discussed in relation to the contrasting thermal regimes of the surface waters characteristic of each species. It is suggested that *A. japonicus* has a more derived reproductive style than *T. trichodon*, including a typical pattern of indirect ontogeny. The remarkable seasonal thermal events in Japanese coastal waters may be responsible for the notable abundance of *A. japonicus*.

Contrast in Reproductive Style Between Two Species of Sandfishes (Family Trichodontidae)

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The family Trichodontidae is a small family of marine fishes endemic to the boreal Pacific comprised of two species, *Arctoscopus japonicus* (Steindachner) from the western Pacific around Japan and *Trichodon trichodon* (Tilesius) from the eastern Pacific, ranging from Alaska to California. As indicated by the common name “sandfishes,” they typically lie partly buried in the bottom (Nelson 1984). Due to peculiar morphological and ecological features, they have been placed at various times in different groups of fishes such as the Percoidei (Matsubara 1963) and Blennioidei (Greenwood et al. 1966).

The biology of *A. japonicus* has been extensively studied because of its special importance to commercial fisheries in northern Japan and Korea (for review, see Ochiai and Tanaka 1986). For *T. trichodon*, however, information is only briefly documented in the literature (Fitch and Lavenberg 1975, Eschmeyer and Herald 1983), except for Marliave (1981) and Bailey et al. (1983) who reported the early life history in detail, and Allen and Smith (1988) who quantitatively illustrated aspects of its zoogeography.

These studies and our own observations, mostly in the northern Sea of Japan, enable us to compare life history traits of these fishes and to discuss probable life strategies associated with zoogeography. The notable fluctuation of the stocks of *A. japonicus* is also considered from the standpoint of comparative ecology.

Comparison between *Arctoscopus japonicus* and *Trichodon trichodon*

Distribution

The family Trichodontidae is restricted in distribution to the coastal boreal regions of the North Pacific between about 35°N and 60°N (Fig. 1). Although Schmidt (1950) reported the occurrences of *A. japonicus* from Akutan Bay and the vicinity of Sitka Island, in the Gulf of Alaska, these records seem questionable (Eschmeyer and Herald 1983). Perhaps these two species have distinct geographical ranges, separated by longitude 160–170°E. *Arctoscopus japonicus* occurs over an extensive area on the western side, including the offshore regions; it is extremely abundant in the Sea of Japan and the Pacific coast off Hokkaido, where catches amounted to 3.8×10^4 tons in 1968 (Ochiai and Tanaka 1986). *Trichodon trichodon* is an eastern Pacific form with a wider range from Kamchatka to southeast of San Francisco, California; there is no fishery for this species, but it is fairly common throughout the coastal waters (Hart 1973, Fitch and Lavenberg 1975, Eschmeyer and Herald 1983, Allen and Smith 1988).

Depth range is variable from the surface to about 400 meters in both species; however, the main life zones are slightly different for the two species. *Arctoscopus japonicus* in the Sea of Japan usually occurs at moderate depths of 200–300 m, with optimum

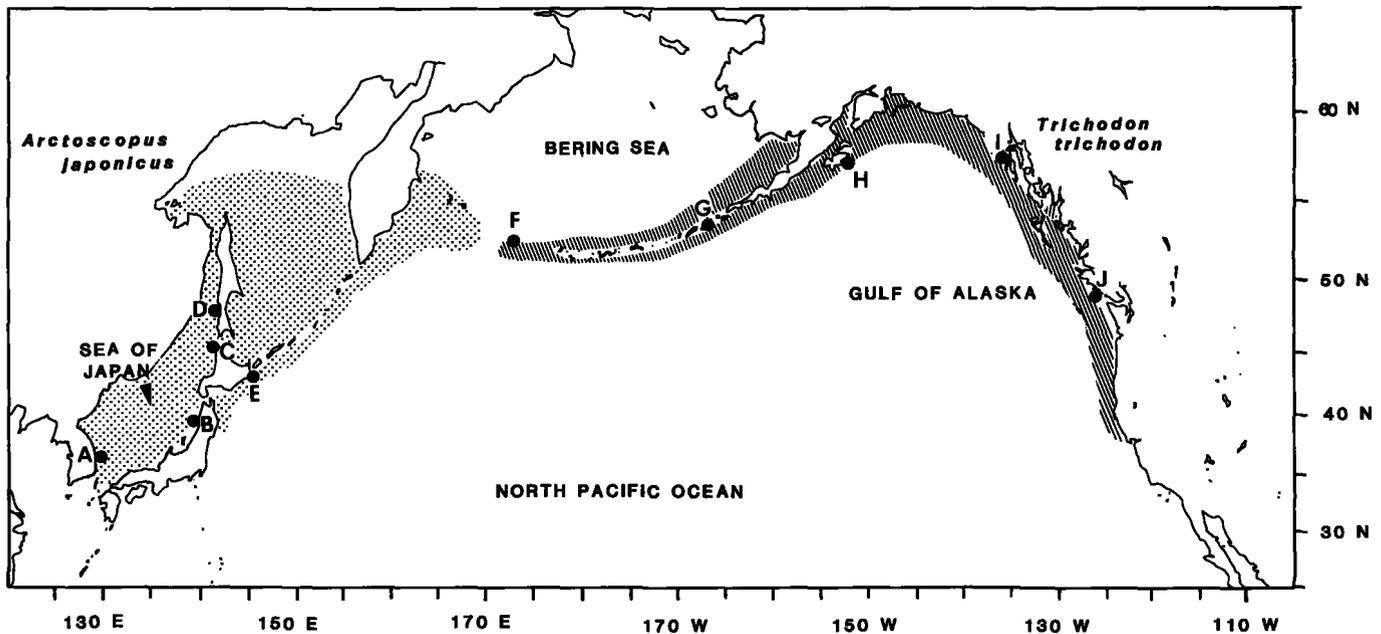


Figure 1

Geographical distribution of two species of sandfishes, family Trichodontidae. (A) Pohang, (B) Akita, (C) Wakkanai, (D) Kholmsk, (E) Nemuro, (F) Attu, (G) Dutch harbor, (H) Kodiak, (I) Sitka, (J) Vancouver. For references, see text.

temperature ranges of 2–5°C (Nishimura 1969). This zone is shifted to a shallower depth of 100–200 m on the Pacific side off Hokkaido (Ochiai and Tanaka 1986). During the spawning season, the adults move into water shallower than about 15 m. In contrast, *T. trichodon* is most frequent on the middle shelf at less than 150 m (Allen and Smith 1988) and spawning is restricted to the intertidal area.

Reproductive ecology

Both species spawn large demersal eggs in rocky, shallow waters during winter months, but interesting ecological differences are found between them, summarized in Table 1. Typically, *A. japonicus* deposits a spherical egg mass tightly on *Sargassum* spp. in such a way that supporting stems pass through the axis of the mass. Successful deposition of secure substrata is of prime importance for survival of eggs, because egg capsules that detach from the substrata become stranded ashore and perish. Onset of spawning at fixed times and locations is characteristic of *A. japonicus*. In the Akita district, for instance, the onset of spawning at major spawning sites rarely fluctuates beyond 1 or 2 weeks from the end of November (Kato 1980).

In contrast, Eschmeyer and Herald (1983) reported that the eggs of *T. trichodon* are laid in a gelatinous mass attached to rocks. One report of a natural spawning was on the wall of a fully exposed surge channel

Table 1

Comparison between reproductive characters of *Arctoscopus japonicus* and *Trichodon trichodon* (after Ochiai and Tanaka 1986; Marliave 1981, unless otherwise indicated below).

Characters	<i>A. japonicus</i>	<i>T. trichodon</i>
Spawning season	Mostly from the end of November to December	Around February
Spawning migration	Conspicuous	Indistinct
Spawning site; substrate	Coastal waters, 0–15 m depth; mostly <i>Sargassum</i> spp.	Intertidal waters, 0–1 m depth; rock
Shape of egg mass	Spherical, 3.3–7 cm in size	Irregular
Diameter of egg	3.3–3.5 mm*	3.52 ± 0.10 mm
Fecundity	600–2300	~1000
Incubation period	56–78 days at 6°–9°C**	1 year (?) at 8°–13°C
Synchronized hatching	No*	Yes; within 24 hours

*Okiyama (unpubl.)

**Maekawa (1985); this indicates the most frequent period.

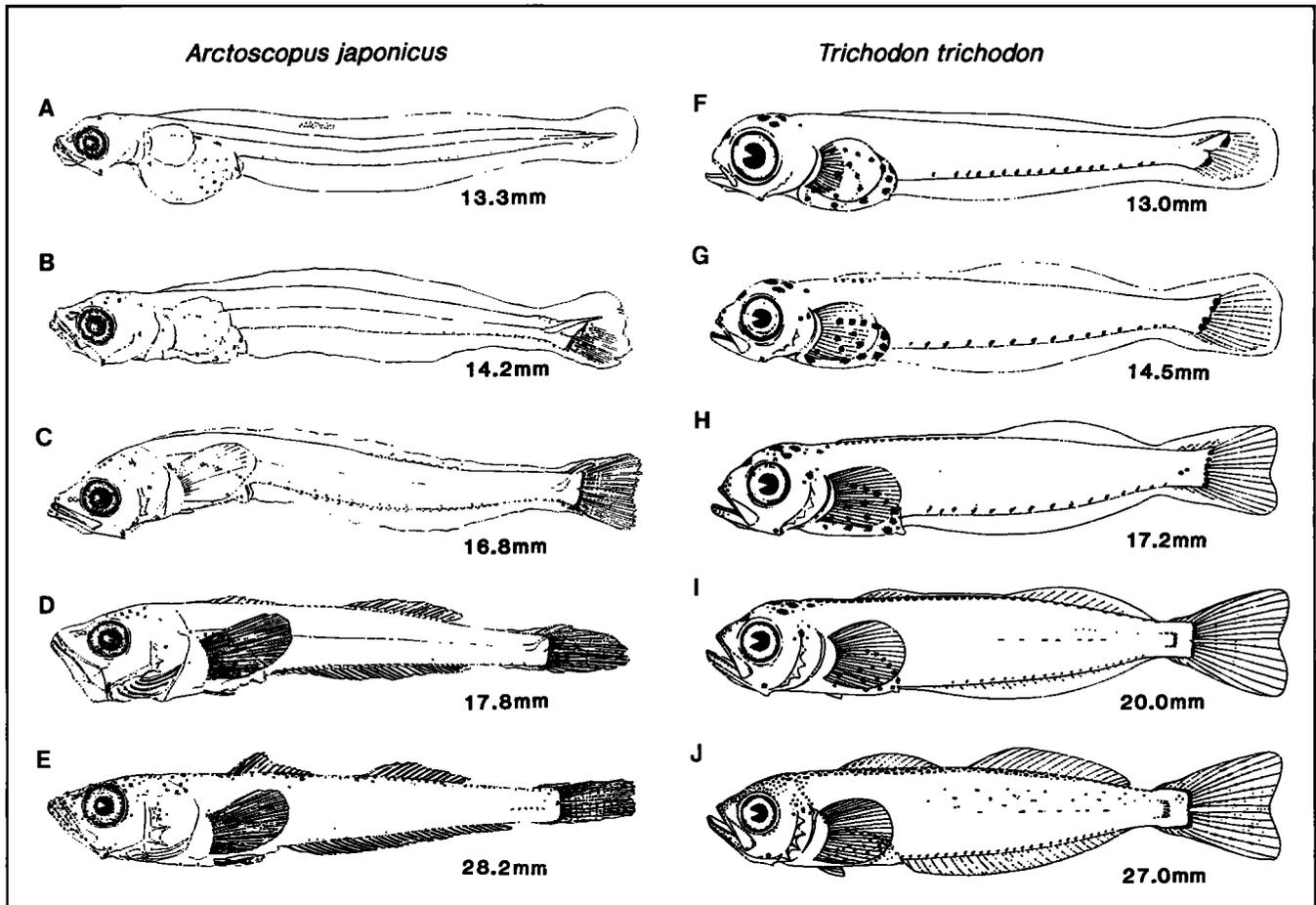


Figure 2

Comparison between early developmental stages of *Arctoscopus japonicus* (left) and *Trichodon trichodon* (right). Size in mm SL; preserved specimens (B–D after Okiyama 1988; F–J after Marliave 1981).

(Marliave 1981). It seems that *T. trichodon* selected this peculiar spawning location because it offered a refuge from egg predation as well as the high flow velocities necessary for respiration (Marliave 1981).

These contrasting reproductive styles should be associated with the different reproductive guilds proposed by Balon (1981, 1984). Although *A. japonicus* fits the "obligatory plant spawners" category, there is no guild relevant to *T. trichodon* within Balon's category of "nonguarders," suggesting its spawning habits may be unique.

Early life history

Larvae and juveniles of both species have been described and illustrated in detail from field and/or laboratory-reared materials (Marliave 1981, Okiyama 1988). In Figure 2, a series of early developmental stages of these species is reproduced from these references, with additional specimens of *A. japonicus* included. Here,

specimens of similar sizes are selected to facilitate interspecific comparison. The early growth of the two species is also compared in Figure 3, based on the laboratory-rearing results; the comparison reveals that *T. trichodon* is consistently larger than *A. japonicus* throughout the 2 months following hatching (Marliave 1981, Maekawa 1985). Despite close resemblances in the general morphology, there are remarkable differences in early developmental patterns between the two species. A few interesting aspects are as follows:

(a) Newly hatched larvae of *A. japonicus*, 13 mm notochord length (NL), are less advanced than those of *T. trichodon*, 13.0 mm standard length (SL); the body is slender, the notochord tip is straight, and fin elements, except several incipient caudal rays, and teeth are absent. In contrast, *T. trichodon* possesses many precocious characters, including a flexed notochord with full complement of principal caudal rays, developing pectoral rays and preopercular spines, in addition to a deeper body, larger eyes, and the presence of

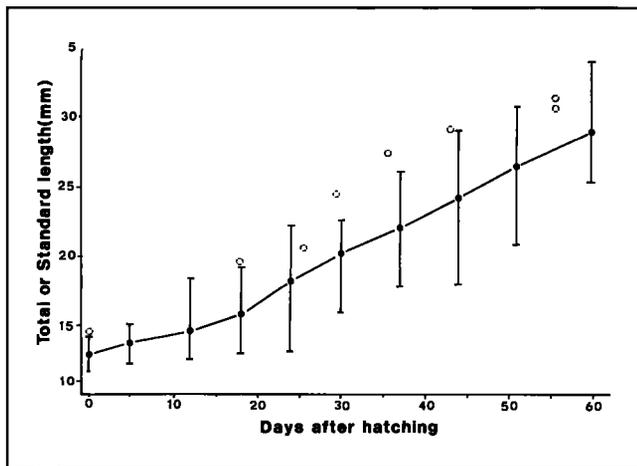


Figure 3

Early growth of laboratory-reared specimens of sandfishes in fresh condition. For *Arctoscopus japonicus*, average (●) and ranges (line) are shown in TL mm (after Maekawa 1985); for *Trichodon trichodon*, individuals (○) are shown in SL mm (after Marliave 1981).

teeth on both jaws. It is clear that these precocious characters are mostly concerned with active swimming. Fast swimming, coupled with large sizes, would not only facilitate successful feeding, but would play an effective role in lowering predation pressure. Slight but distinct size and development differences at hatching between the two species, therefore, are among the most important aspects of their early life histories.

(b) Orders of fin ray ossification of the two species can be derived from Table 2, although the available size series of *T. trichodon* (Marliave 1981) is somewhat limited. Except for the precocious caudal and pectoral fins in *T. trichodon*, all other fin meristics are formed in smaller specimens of *A. japonicus*. The entire size ranges for fin development are 14.9–19.0 mm in *A. japonicus* versus 13.0–30.0 mm in *T. trichodon*. Possible sequence of fin ossification is caudal-pectoral-anal-2nd dorsal-1st dorsal-pelvic for both species.

(c) Larvae of both species are sparsely pigmented and lack extensive melanin on the lateral side of the tail. Pigmentation is generally heavier in *T. trichodon* than in *A. japonicus*. In particular, earlier development of distinct spots along the anterior dorsal margin of *T. trichodon* is remarkable because this character first occurs after transformation into juveniles in *A. japonicus*.

(d) According to the conventional definitions of early developmental stage, transformation from larval to juvenile stages occurs at about 20 mm in *A. japonicus* versus about 30 mm in *T. trichodon*. However, *T. trichodon* is distinctly more advanced than *A. japonicus* in every early-life-history trait, except formation of fins other than the caudal and pectoral.

Table 2

Comparison between fin formation of *Arctoscopus japonicus* and *Trichodon trichodon* (mm SL).

Characters	<i>A. japonicus</i> *		<i>T. trichodon</i> **	
	start	finish	start	finish
1st dorsal	16.2	19.0	20.0–	28.0
2nd dorsal	16.2	17.8	20.0	27.0
Anal fin	16.2	17.8	20.0	27.0
Pectoral	14.9	17.8	13.0	17.2
Pelvic	16.8	19.0	27.0	30.0
Caudal (principal)	14.9	14.9	13.0	13.0

*Original data from specimens of the Sea of Japan.

**After Marliave (1981), slightly modified on the basis of two newly hatched larvae (13.0, 13.2 mm SL; preserved) provided by him.

Major contrasts in their ontogenetic properties may be summarized as follows: *A. japonicus* has a distinct, but truncated, metamorphosing phase (20–30 mm SL) closely corresponding to the change from pelagic to demersal life (Minami and Tanaka 1985, Okiyama unpubl.); in contrast, *T. trichodon* has a less distinct metamorphosing phase (30–50 mm SL) without any ecological shifts other than possible decrease of schooling tendencies (Marliave 1981, Bailey et al. 1983), although it starts burying itself in the sand at 55–60 mm SL (J.B. Marliave, Vancouver Aquarium, P.O. Box 3232, Vancouver, B.C., Canada, pers. commun., April 1989).

Contrast in life history strategy

Notwithstanding the close systematic relationship between *A. japonicus* and *T. trichodon*, there are many life history features unique to each species, particularly with respect to the reproductive styles as discussed earlier. The terms and duration of their early developmental stages are shown in Figure 4, revealing that the egg stage of *T. trichodon* is almost four times longer than that of *A. japonicus*; however, the time when the larvae of both species appear is restricted to the spring seasons. The mechanism of this synchronized hatching is unknown, but plausible advantages are apparent. It is obvious that spawning substrates play an important role in producing these contrasting patterns of development. Perhaps the specialized mode of egg deposition unique to *A. japonicus* has evolved in close association with the abundant substrates represented by *Sargassum* spp., whereas, as suggested Marliave (1981), most plant substrates would have been too transitory to act as an egg deposition site for *T. trichodon*.

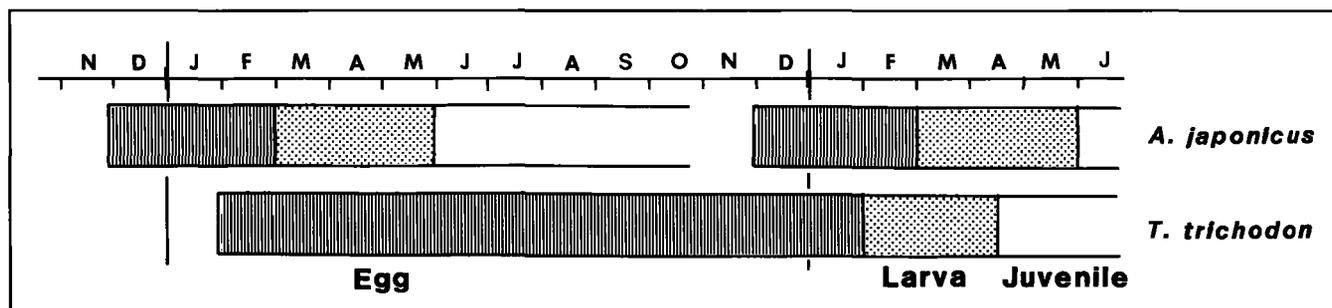


Figure 4

Comparison between terms and duration of early developmental stages of *Arctoscopus japonicus* and *Trichodon trichodon*. For sources, see text.

These ecological differences in spawning are compared with seasonal variations of the surface water temperatures among several stations covering most of the distribution areas of the two species (Fig. 5). By inspection, the location of two groups of stations may be recognized as corresponding to the zoogeography of the two species. Temperature ranges for *A. japonicus* are uniformly broader than those for *T. trichodon*: -2° - 10° C to 18° - 25° C versus 2° - 7° C to 9° - 14° C. Furthermore, temperature differences where the two species occur are particularly great during the warmer seasons. In the Sea of Japan, *A. japonicus* apparently copes with these extreme environmental conditions by precisely timing their early ontogeny to cold seasons and by gradually shifting the habitat toward deeper levels (up to 200-300 m) as growth proceeds (Nishimura 1969, Minami and Tanaka 1985).

Alternatively, the lowest temperature ranges of the eastern Pacific stations lie intermediate to those of the western Pacific stations. This stands in sharp contrast with the highest temperatures, which are not overlapping. Considering the year-round occurrence of the eggs of *T. trichodon* in the rocky intertidal area, it is quite natural to suppose that this species demands a particular set of physical environmental conditions for the specific spawning site, such as less variable water temperatures and above-freezing temperatures. These specific thermal conditions may also be responsible for the indistinct ontogenetic migration of *T. trichodon*.

Although there is no reliable information on the abundance of *T. trichodon*, except catch data of Allen and Smith (1988), *A. japonicus* surely has greater stocks than the former species. Total landings of *A. japonicus* in the Sea of Japan by Japanese vessels peaked at 3.3×10^4 tons in 1966. Of these, 2.1×10^4 tons were caught in the restricted area along the northwestern district of the Japanese mainland, namely, Akita Prefecture, where one of the biggest spawning grounds occurs regularly (Okiyama 1970, Kato 1980).

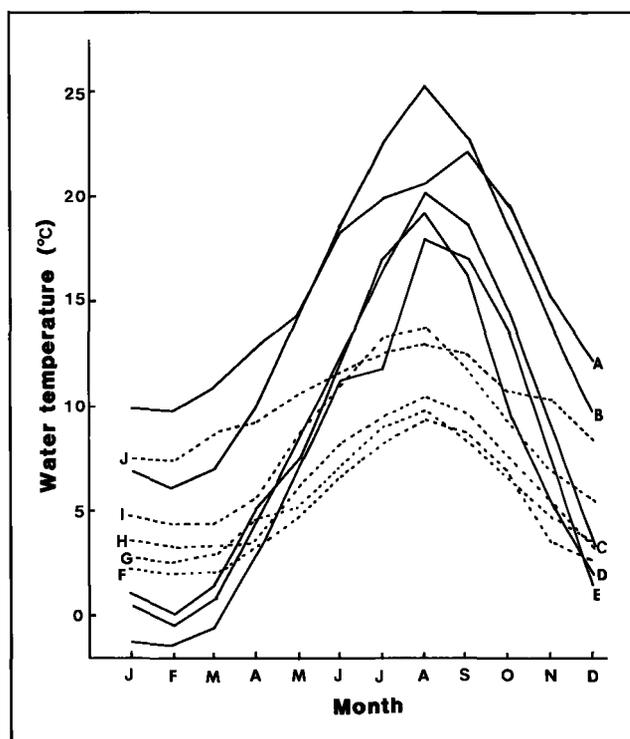


Figure 5

Seasonal patterns of surface-water temperatures from ten stations within the ranges of *Arctoscopus japonicus* (A-E, solid lines) and *Trichodon trichodon* (F-J, dotted lines) (adapted from Wadachi 1960). For locations, see Figure 1.

Figure 6 shows the long-term fluctuations of the catches of *A. japonicus* in this district. Coastal catches, comprised exclusively of fully matured specimens, are separated here from the total catches. Drastic changes in catches occurred during a 30-year period with peaks occurring around 1965-68 and 1974-75. The decrease between these peaks is slight as compared with the events in other periods such as around 1955 and after 1978. In 1984, the coastal catch dropped to a low of

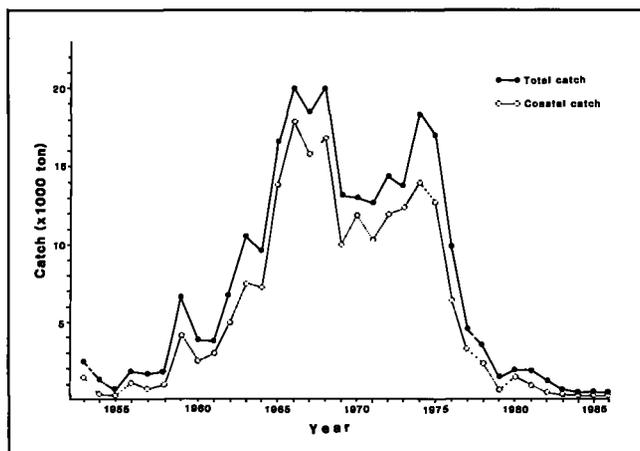


Figure 6

Fluctuation of the catch of *Arctoscopus japonicus* in Akita district, the northern Sea of Japan (after Ikehata 1987).

only 10^3 tons from the maximum record of about 18 000 tons in 1966; the maximum/minimum ratio was about 180. Such drastic fluctuations may be extremely rare among demersal fishes, and a ratio of about 180 would be exceptionally great even among pelagic fish stocks (Funakoshi 1988). Usually these fluctuations are attributed to heavy fishing on a parent stock after the appearance of several poor year-classes, or conspicuous recruitment success in particular periods (Lasker 1981). It is also generally accepted that success or failure in survival during the early period of ontogeny is critically important for successful year-classes.

In addition to the early-life-history traits, rearing experiments suggest that early larvae of *A. japonicus* have many adaptive features promoting survival. They include an early onset of exogenous feeding paired with a long period of mixed feeding (mixed endogenous and exogenous feeding) in larvae 3 days after hatching to early juveniles of about 20 mm SL (Maekawa 1985). Likewise, Marliave (1981) observed an early onset of first feeding in *T. trichodon*, at about 48 hours after hatching in an aquarium. Prolonged mixed feeding is also possible in this species. This may suggest that starvation is not usually the main cause of mortality in early stages. Concerning other mortality factors, such as predation during the early larval period, no reliable information is available for either species.

The importance of mixed feeding as a feature of a developing organism was stressed by Balon (1986). He suggested that the flexibility provided by a varying duration of mixed feeding can facilitate changes in the entire life history of the species. In view of the characteristic mixed-feeding feature of early stages of these two species, their contrasting ontogeny seems to be largely explained within this context. Possibly, slight

differences in size and yolk volume in newly hatched larvae of the two species are responsible for creating the observed dichotomy in their life history patterns: *A. japonicus* developed the indirect type of ontogeny, having a distinct pelagic larval stage and demersal juveniles with intervening metamorphosis; *T. trichodon* developed the rather direct type of ontogeny having no distinct pelagic larval stage.

These contrasting life history patterns may be closely associated with the probable differences of their stock sizes. For example, the highly derived nature of ontogeny in *A. japonicus*, including the locally restricted spawning grounds, the specialized spawning method, the remarkably precise spawning season, and the typical sequence of early developments, may imply a high likelihood of a greater sensitivity of stock size to environmental changes. Of these features, the presence of so-called "first metamorphosis" (Youson 1988) should be emphasized because this phase, although less drastic than the others, is expected to play a significant role in regulating successful transition events according to varying environmental situations.

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