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Life history of Pacific rainbow smelt *Osmerus dentex* in Funka Bay, Japan

（噴火湾におけるキュウリウオ *Osmerus dentex* の生活史）

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SUMMARY

I. Introduction

Pacific rainbow smelt *Osmerus dentex* is one of the Osmeridae fishes distributed around Hokkaido Island, northern Japan. Recently, the natural resources of important commercial species of the family such as shishamo *Spirinchus lanceolatus* and capelin *Mallotus villosus* have been reported to decrease due to overfishing and destruction in living environment. The understanding about the biological and ecological features of *O. dentex* is needed not only to fulfilling lacks in the knowledges of the Osmeridae, but also for sustainable resource management of this this species, as well as the other species in the family. This thesis aims to clarify the growth process, feeding habits, and early survival process of *O. dentex* with ecological approaches for suitable fisheries management and future seed release.

II. Materials and methods

O. dentex were collected from T/S *Ushio-maru* (179 tons) of Faculty of Fisheries, Hokkaido University with two types of otter trawl nets in Funka Bay from December 2015 to May 2021. In addition, scoop net sampling was carried out at the mouth of the Yamazaki River in late April and mid-May in 2019. Samples were measured body sizes, sexed, weighed liver and gonads, and removed stomachs, scales, and otoliths. The reliability in age determination between scale and sagittal otolith was compared by evaluating the precision among three independent readers based on the percentage of agreement (PA), coefficient of variation (CV), and average percentage of error (APE). The growth models of fish were fitted with the Gompertz, logistic, von Bertalanffy, and Richard's growth equations; and the best fitted growth model was selected by using r^2 and AIC values. Feeding habit of *O. dentex* was assessed by analyzing the stomach content. The experiments were conducted to evaluate the effects of different temperatures (8, 10, 12 and

14°C) and salinities (0, 8, 16, 24 and 32) on hatching success and embryonic period of *O. dentex*. The experiment to evaluate the effects of different salinities (0, 8, 16, and 24) on the survival rate and the growth of *O. dentex* larvae until 15 days after hatchings (DAH) was also conducted.

III. Results and discussion

Annual increment on otolith was verified for growth analysis for *O. dentex* because otolith ageing was founded more reliable than scale ageing with less error among readers. The Gompertz growth equation was judged as the best fit model for growth curves of *O. dentex* by r^2 and *AIC* values, however, there was little difference in goodness of fit among Gompertz, logistic, von Bertalanffy, and Richard's growth equations. The maximum age and body size of *O. dentex* in Funka Bay and the mouth part of the Yamazaki River were generally lower than those of *O. dentex* collected in the Beaufort Sea off Alaska, Norton Sound, and southeastern Chukchi Sea in the Arctic Ocean form other studies. The growth rate in Funka Bay was higher than other areas. The difference might be caused by latitudinal effects, food availability, and photoperiod between areas.

Ontogenetic shift in diet was detected in *O. dentex* in Funka Bay and the mouth part of the Yamazaki River. The smaller sized *O. dentex* (< 156 mm SL and 184 mm TL) fed mainly on Decapoda Natantia, Mysidacea, and Amphipoda Gammaridea, and the larger sized one (≥ 157 mm SL) fed mainly on Pisces (fishes such as Japanese anchovy *Engraulis japonicus*, walleye pollock *Gadus chalcogrammus* juveniles, and other three demersal fish juveniles). High percentages of empty stomachs in *O. dentex* in Funka Bay and the Yamazaki River (73% and 88% in the frequency of vacant stomachs, respectively) during spawning period (April-May) were presumed to be caused by low prey requirement during spawning season, the low abundance of walleye pollock

juveniles in the environment and the fact that Japanese anchovy was not distributed at all in the low water temperature environment.

Embryos of *O. dentex* were successfully hatched at the temperature range of 8-14°C, and the salinity range of 0-16 but not in 32. The incubation period of embryos was affected by temperature (14-31 days at 8-14°C), but not by salinity in 0-24. The biological zero degree at which embryogenesis ceases was estimated to be 3.4°C, and the cumulative temperature unit was calculated to be 220 ± 25.6 day·°C. Early stage of *O. dentex* larvae of 15 days after hatching (DAH) obtained highest survival rate at rearing in 0-16 salinities, and the highest growth rates showed at 8 and 16. The osmoregulation organ systems in early larval stages might be still not sufficiently developed to encounter osmoregulatory stress in a high salinity environment, and hence, cause mortality. It is suggested that an acclimation in *O. dentex* larvae is necessary for survival the larvae into brackish water (may be into estuary and coastal area) until 15 DAH at least.

The noticeable characteristic of *O. dentex* is larger body size than the other five species of Osmeridae distributed around Hokkaido, and the maximum size of *O. dentex* is 1.5–2 fold larger than the others. With the regarding to the feeding habits, *O. dentex* is the only species that fed mainly on fishes, and this feature is probably the reason causing the prominent size of *O. dentex*. It is interesting that *O. dentex* is mostly absent or rare in the western and northern sides of Hokkaido. Funka Bay has a maximum depth of 98 m and a greater area of shallow water (70 m or less) than other water areas in Hokkaido, and this geographical feature may be suitable for *O. dentex*.

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Nam

Hakodate, June 2021

CHAPTER 1. GENERAL INTRODUCTION

1.1. Background

Rainbow smelt *Osmerus dentex* is one of anadromous fish species and is distributed in the northern Pacific coast from east Korea Peninsula, Hokkaido, Sakhalin, Alaska, to Vancouver Island of Canada (Becker 1983; Morrow 1980). The Funka Bay stock of this species come into the rivers in nighttime for spawning from late April to mid-May (Inokuchi et al. 1997), and yolksac larvae hatched from eggs return to the sea. Stock identification by numerical characters (fin rays, vertebrates, gill raker, and pyloric caeca; Horikawa and Kyushin 1987), egg size and fecundity (Horikawa 1988), and oocyte development and spatial distribution in Funka Bay (Inokuchi et al. 1997) have been clarified, however ecological feature, e.g., feeding habits and growth trajectory are not known. To utilized fisheries resource and the management of this species, we must elucidate aspect of ecological features in fish community from prey-predation interaction and growth processes in wildlife. In addition, large population fluctuation occurs in early life stages, like egg, larval, and juvenile periods in general. However, the early life history and survival process of rainbow smelt is roughly unknown. We need to clarify the survival strategy of rainbow smelt in egg stage in freshwater and larval stage in brackish and salt waters with physiologic advantages for survival.

1.2. General objectives

The aims of this study are to clarify the growth process, feeding habits, and early survival process of rainbow smelt *O. dentex* used with ecological approaches for suitable fisheries management and future seed release. To obtain these objectives, the following works had been conducted and presented in the following chapters:
Chapter 3: **Age and growth of Pacific rainbow smelt *O. dentex* estimated from scales and otoliths in Funka Bay and the Yamazaki River, Japan.**

The objectives of this chapter were to compare the reliability between ageing *O. dentex* using sagittal otolith and scale methods, and to describe the growth

features of *O. dentex* collected in Funka Bay and at the mouth part of the Yamazaki River.

Chapter 4: **Feeding habits of rainbow smelt and special reference to fish predation in Funka Bay, Japan.**

The aims of this chapter are to clarify the diet and feeding habits of *O. dentex* in Funka Bay, and to elucidate the factors that achieve high growth rate from the feeding ecology.

Chapter 5: **Effects of environment on the embryo and larval development of *O. dentex***

To determine the effects of temperature and salinity on egg survival, as well as the influence of salinity on the early life development of this species, rearing experiments of *O. dentex* were carried out in this chapter.

Chapter 6: **Conclusions, General Discussions, and Future research**

This chapter summarizes the results with general discussions and suggested the future research.

CHAPTER 2. LITERATURE REVIEWS

2.1. Smelts family (Osmeridae)

2.1.1. Classification of Smelts

Kingdom: Animalia

Phylum: Chordata

Class: Actinopterygii

Order: Osmeriformes

Family: Osmeridae

Genus: *Allosmerus*

Genus: *Hypomesus*

Genus: *Mallotus*

Genus: *Osmerus*

Genus: *Spirinchus*

Genus: *Thaleichthys*

According to Kendall (1926), the smelts' family (Osmeridae) is a group of fishes of wide geography distribution in the northern latitudes. The smelts distributional belt encircle in the Northern Hemisphere with the distribution is recorded in the coasts of North Atlantic, North Pacific and Arctic Ocean. The systematic uncertainly occurs at several taxonomic levels (Ilves and Taylor 2009). Smelts were originally classified to the salmonid genus *Salmo* by Linnaeus (1758). The separate osmerid genus *Osmerus* was then introduced by Cuvier in 1817, albeit still in Salmonidae; in 1913 osmerid was removed to family Osmeridae (Ilves and Taylor 2009; Begle 1991). Currently, family Osmeridae include 6 genera with 15 species, which are: *Hypomesus* (5), *Mallotus* (Capelin) (1), *Osmerus* (4), *Thaleichthys* (Eulachon) (1), *Allosmerus* (1), and *Spirinchus* (3). The term Osmerus originates from Greek word Osme, which means "bad smelling" due to most of the fishes in family have strong odor similar to freshly cut cucumbers when taken out of water. Most species are anadromous (spawn in freshwater and mature in the marine environment), but two

are strictly marine (*Allosmerus elongatus* and *Spirinchus starksi*), one strictly freshwater (*Hypomesus olidus*), and others have populations that appear to have secondarily become freshwater residents (*Hypomesus nipponensis*, *Osmerus eperlanus*, *Osmerus mordax*, and *Spirinchus thaleichhtys*; Ilves and Taylor 2009; Nelson et al. 2016).

Osmerus is one of the important genera of the smelts' family. The taxonomical inter-relationships among species of the genus *Osmerus* have been the subject of controversy. In 1963, McAllister hypothesized that genus Osmerus have only one wide-ranging species *O. eperlanus*; but divided the species into two sub-species, *O. e. eperlanus* and *O. e. mordax*. Scott and Crossman (1973) divided the genus into two species: *O. eperlanus* of the European Atlantic coast and *O. mordax* of the Pacific, Arctic and western Atlantic coasts; which the *O. mordax* was divided into two sub-species, the western Atlantic form *O. m. mordax* and the Pacific and Arctic form *O. m. dentex*. Taylor and Dodson (1994), based on examining the mitochondrial DNA (mtDNA), divided *Osmerus* into three species: north-eastern Atlantic form *O. eperlanus*, north-western Atlantic form *O. mordax*, and Pacific/Arctic form *O. dentex*; and suggested that *O. mordax* and *O. dentex* shared a common ancestor than either has with *O. eperlanus*. However, Mecklenburg et al. (2011), based on the results of DNA barcoding (cytochrome c oxidase 1 gene; CO1 sequences), suggested that *O. eperlanus* is more genetically similar to *O. dentex* than *O. mordax*. Recent research by Balakirev (2018), with the complete mitochondrial genome sequences, confirmed that all of them are separate biological species.

Currently, four species of genus *Osmerus* have been accepted as: Rainbow smelt *O. mordax* (Mitchill 1814), European smelt *O. eperlanus* (Linnaeus 1758), Arctic rainbow smelt *O. dentex* (Steindachner & Kner 1870), and Pigmy smelt *O. spectrum* (Cope 1870) (Fishbase 2021; Encyclopedia of Life 2021). The pigmy smelt *O. spectrum,* which is often miss distinguished with land-locked *O. mordax*, is a freshwater fish distributes only in North America and less interested (Taylor and Bentzen 1993; Bradbury et al. 2011).

2.1.2. Pacific rainbow smelt

Common name: Pacific rainbow smelt, Arctic smelt, toothed rainbow smelt, Asiantic smelt, and kyuuriuo (in Japanese).

Scientific name: *O. dentex* Steindachner and Kner 1870. In Japan, Pacific rainbow smelt were previously treated as *O. dentex* by Jordan and Snyder (1902) and Hubbs (1925). Lately, the fish were identified as *Osmerus eperlanus mordax* Mitchill (Yanagawa 1978; Horikawa and Kyushin 1987; Horikawa 1988; Inokuchi et al. 1997; Takahashi et al. 2016). Recently, Motomura (2020) confirmed that only one species of rainbow smelt occurs in Japan and identified as *O. dentex*.

Distribution: Pacific rainbow smelt *O. dentex* Steindachner and Kner 1870 has wide distribution in the North Pacific regions from the Bering Sea southward to the Wonsan coastal area (North Korea) and Hokkaido (North Japan); the Sea of Okhotsk to Barkley Sound (British Columbia), northward to the Bering Sea, and the Arctic Ocean from the White Sea to the Chukotka Sea (eastern Siberia) (Fig. 2-1).

Morphology: *O. dentex* is a small, slender fish with olive green above, shading to silvery below, a bright clearly bounded longitudinal silvery band; speckled with black on top of head, chin and upper part of body, more plentifully along mid-dorsal line. Body elongates, head moderately long; eye moderately large; snout elongate and pointed; mouth large, upper jaw about reaching vertical from posterior margin of eye, lower jaw protruding, maxillary extends to middle or beyond of eye. Large teeth on vomer, palatine, pterygoid, basibranchial, dentary, maxillary, premaxillary, and tongue, teeth especially enlarged on tongue and front of vomer. Formation of scales begins when body length from 26 mm (minimum length of fish with scales) to 31 mm (maximum length of fish without scales). Scale is cycloid, thin, and deciduous; 66 to 69 in lateral line, 13-28 pored scales in the lateral lines. Pectoral rays 12-14; dorsal rays 8-11, no dorsal spine, dorsal origin slightly in front of pelvic origin; anal rays 12-16, no anal spine; adipose fin is small, sickle shape; caudal forked, with 19 rays. Vertebrae 58-70, usually 60-66. Intestine short, pyloric caeca 4-8 (Hubbs 1925; Hart 1973; Vasilets 2000; Mutoh 2003a; Kottelat



Fig. 2-1. Distribution map of *O. dentex* (Vasilets 2000; Kottelat and Freyhof 2007; Kovpak et al. 2011; Skurikhina et al. 2018; Fishbase 2021; Semenova et al. 2021)

and Freyhof 2007).

Habitat: Brackish water of estuaries, lagoon, coastal shallows and bays; freshwater in inland waters of rivers, streams. Spawn in clear water, over stone-gravel bottom at depth 0.2-0.5 m.

Biology: Pacific rainbow smelt is anadromous, in spring, the fish enters rivers for spawning. Spawning migration usually starts in April – May, 2-3 days after ice melting at the temperature of 2-3°C. Distance of migration depends on availability of spawning site, can up to hundreds km. Fish spawns at 7-14°C; spawning takes place mainly at night; the eggs are released in clusters and the milt is released simultaneously; the spawners return to the sea soon after spawning (Scott and Crossman 1973; Mutoh 2003a; Kottelat and Freyhof 2007; Datsky 2017). Vasilets (2000) described the migration spawning cycle of *O. dentex*, with the example of smelt in Sakhalin-Kuril shelf, as the follows:

1) *Post-spawning migrations* (second half of June to first half July). Take a relatively short period of time within two to three weeks. The fish is kept at depths of up to 20 m near the mouths of the main rivers, adapting to the marine environment and restoring the body after spawning.
2) *Summer forage migrations* (July to September). Fish retreats to the coastal area on depth up to 50 m.
3) *Autumn forage migrations* (October to mid-January). Characteristic of this period is the accumulations of smelt with high density in the offshore sections of the shelf (isobaths up to 90-100 m).
4) *Winter forage migrations* (end of January to March). The fish migrates to depths up to 15 m and actively feeds in the highly productive under-ice layer water.
5) *Pre-spawning migrations* (April). The spawners concentrate in areas of the main spawning rivers at depths of up to 50 m.
6) *Spawning migrations* (end of April to June). Feeding completely stops. The entry of spawners into the rivers is noted.

In Hokkaido, Japan, *O. dentex* is reported to spawn from late April to mid-May with the main spawning ground is the rivers in the western coast of Funka Bay (Inokuchi et al. 1997). *O. dentex* eggs is adhesive; fecundity of fish depends upon the size of females ranging from 38,800 to 88,000 eggs per female (range of body length: 177-230 mm); numbers of eggs vary from 2,460 to 3,610 eggs per 1.0 g of ovary (Horikawa 1988). The eggs size is 0.76-1.21 mm in diameter; hatched in 2-3 weeks after fertilization depending on temperature (Horikawa 1988, Kottelat and Freyhof 2007).

Larval and young smelt feed on Copepoda, Cladocera, Rotatoria, eggs, and algae. Adult in seawater feeds mostly on small fishes (Pisces), shrimp (Decapoda Natantia) and mysids (Mysidacea), Copapoda, Amphipoda, as well as molluscan shellfish (Gastropoda and Bivalvia), crabs (Decapoda Reptantia), squid (Mollusca Decapoda) and worms (Polychaeta). The feeding intensity of *O. dentex* varies during the year, the amount of consumed food decreased as the fish matures and ceasing feeding during spawning. Feeding peak occurs at night, during maximum tide; daily rhythm of consuming has a monocyclic character (Hart 1973; Scott and Crossman 1973; Karpenko and Vasilets 1996; Mutoh 2003a; Kottelat and Freyhof 2007; Samatov 2005).

2.2. Funka Bay

Funka Bay, has also been known as Uchiura Bay or Eruption Bay, is a semi-enclosed bay situated on the south-western coast in Hokkaido Island, northern Japan. The bay has a bowl-shaped bottom that reaches a depth of 98 m and is delineated by the line connecting Cape Chikyu and Cape Suna and joined to the northwestern North Pacific Ocean by an 80 m deep sill (Ohtani and Kido 1980). Due to its characteristic (semi-enclosed), Funka Bay is weakly influenced by terrestrial materials from the river discharge but is strongly affected by intrusive water masses (Ohtani and Akiba 1970; Sasaki et al. 2005).

Water temperature and salinity of Funka Bay varies with the depth of water

column (Fig. 2-2). The hydrographic conditions of Funka Bay are controlled mainly by two water masses originating from the North Pacific western subtropical water and North Pacific western subarctic water. Tsushima Warm Current, which flows along the western coast of Honshu Island in the Sea of Japan and passes through the Tsugaru Strait to the Pacific Ocean. This water (called the Tsugaru Warm Water; TWW) is characterized by a high salinity (≥ 33.8) and temperature (≥ 6°C) intruding in Funka Bay from late summer to late autumn (Ohtani, 1971; Ohtani and Kido, 1980). TWW stagnates in the whole bay during winter. The other water mass is the cold and less saline Oyashio Coastal Water (OCW; ≤ 33.3 in salinity and ≤ 3°C); enters the bay from late January through February (Ohtani, 1971; Ohtani and Kido, 1980; Kido and Ohtani 1981).

Funka Bay are reported to accumulate high concentration of nutrients and particulate organic matter in the basin water such as iron (Fe and Fe^{3+}), PO_4-P, Nitrate, Chlorophyll-*a*, and dissolved organic matter (Kido and Ohtani 1981; Iinuma et al. 1998; Kuma et al. 2000; Sasaki et al. 2005). These nutrients in the water support the growth of phytoplankton and increase their abundance. In most years, a phytoplankton bloom consisting mainly of diatoms occurs in the surface layer, covering most of the bay from early March to early April (Ooki et al. 2019). The magnitude and species composition this spring bloom in Funka Bay is considered to affect by the intrusion of OCW. The spring bloom in turn affects the production of herbivorous zooplankton, such as copepods, flagellates and ciliates, and animals at higher trophic levels, such as walleye pollock, for example (Shinada et al. 1999).

Fishes assemblages inhabiting in Funka Bay belong to 50 families, including 116 genera and 141 species. Of which, 85 species are temperate forms, and the remaining are boreal species (Hikita 1951). The inside shallow water area of Funka Bay is considered as the nursery grounds for commercially important fish species such as walleye pollock *Gadus chalcogrammus*, flathead founder *Hippoglossoides dubius*, stone flounder *Platichthys bicoloratus*, and Japanese anchovy *Engraulis japonicus*. And hence, these fishes' larvae are abundant in Funka Bay (Kinoshita 1962; Hayashi

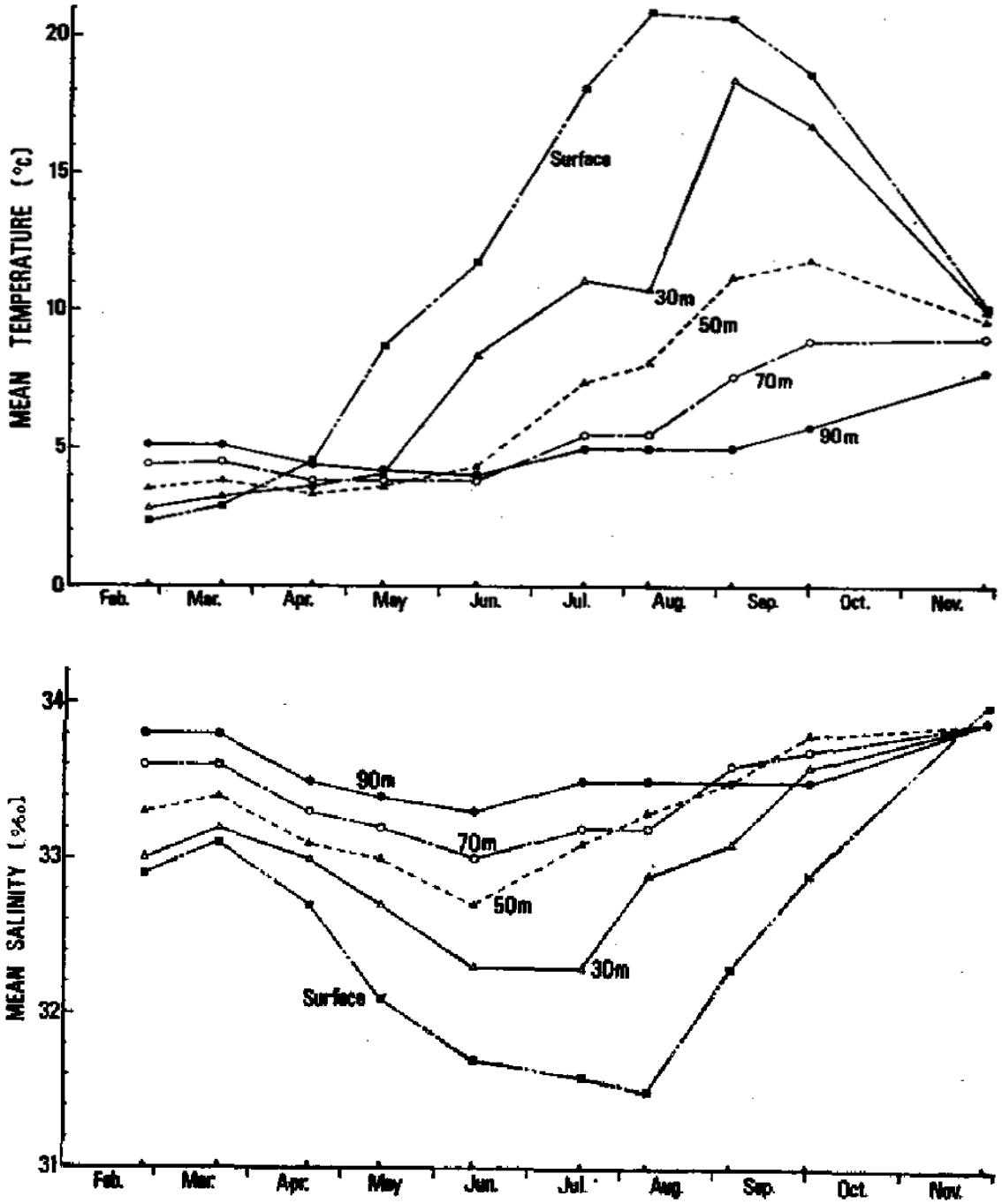


Fig. 2-2. Mean water temperature and salinity at each depth layer in Funka Bay (Kido and Ohtani 1981).

1963; Maeda et al. 1976; Nakatani and Maeda 1987; Hashimoto et al. 2011; Kawauchi et al. 2011; Kano et al. 2015).

2.3. Literature reviews on studies of age estimation, growth, feeding, and life history of fish.

2.3.1. Age and growth studies of fish

Age and growth studies on fishes are very essential in planning and managing of fish not only in aquaculture but also in fishery research (Abu El-Nasr 2017). The exact age determination of fish is one of the most important elements in the study of their population dynamics, and it forms the basis for calculations leading to a knowledge of the growth, mortality, recruitment and other fundamental parameters of their populations (Holden and Raitt 1974). Age-structure model, which attempts to capture the composite behavior of the cohorts making up a population, used in the analysis of yield-per-recruit (Haddon 2001). Sustained yield management of fish resources, especially which are heavily exploited, requires the scientific information about age and growth of them. The age of fish can tell their longevity, age at maturity, age at migration to sea and return to freshwater (or vice versa), and age when they are recruited to the fishery. Carefully determined fish age data are essential for the calculation of growth, mortality rates and recruitment of fish population, which are essential to the proper assessment and management of fisheries (Summerfelt 1987).

Various methods can used for determining age of fish, they can be grouped into three basic methods: 1) direct observation of fish of known age; 2) studies of fish length-frequencies and; 3) study of ring formation in hard structures of fish (Lux 1971).

Direct observation of fish of known age

In this method, known age fish are reared in pond of aquarium, age and length are determined simply by catching and measuring the fish. Tagging (physically or chemically), releasing, and recapturing of known age individuals is an extension of

this technique. The method is considered the most reliable methods in age determination of fish. The disadvantages of this method are followings, growth rates of fish under artificial conditions may differ from their natural environment; rearing technique of some species may be difficult; tagging may require careful handling and large number of released fish (Lux 1971; Campana 2001).

Studies of length-frequency distribution

Length-frequency distribution is obtained by plotting numbers of fish in each of length intervals, different peaks represent the average length in a separate age group because the restricted range of lengths within each age group (Kumar and Adams 1977; Campana 2001)

Studies by using hard structures

Similar to the tree rings, seasonal changes in growth rate of fishes are reflected in bands or zones on hard structures of fish. These growth bands or zones are usually formed periodically, usually once a year, which called as annuli (Lux 1971; Casselman 1990; Campana 2001). Several hard structures are used for age determination in fish such as scales, otoliths, vertebrae, fin rays, cleithra, and opercula (Beamish and McFarlane 1987; Stevenson and Campana 1992; Campana 2001; Panfili et al. 2002; Katayama 2018). The preparation procedures for different hard structures are summarized by Gaamour and Khamiri (2004) in Fig. 2-3. Otoliths and scales are the two structures most widely used for age determination (Holden and Raitt 1974, Stevenson and Campana 1992; Campana 2001).

The advantage of scales ageing is harmless to fish; scales collecting and preparing are relatively quick and easy, and required simple tools. However, age determination by scales does also have some disadvantages. Some scales of fish, such as trout, shows unclear seasonal differences between growth rings; scales of sunfish and bass are often unable to detect the differences in growth rings. Resorption and erosion in scales is another drawback in scales ageing; many fish are able to re-absorb scales to replace the lost ones resulting in underestimation of fish age, especially in older fish and slow growing fish (Waston 1967; Lux 1971;

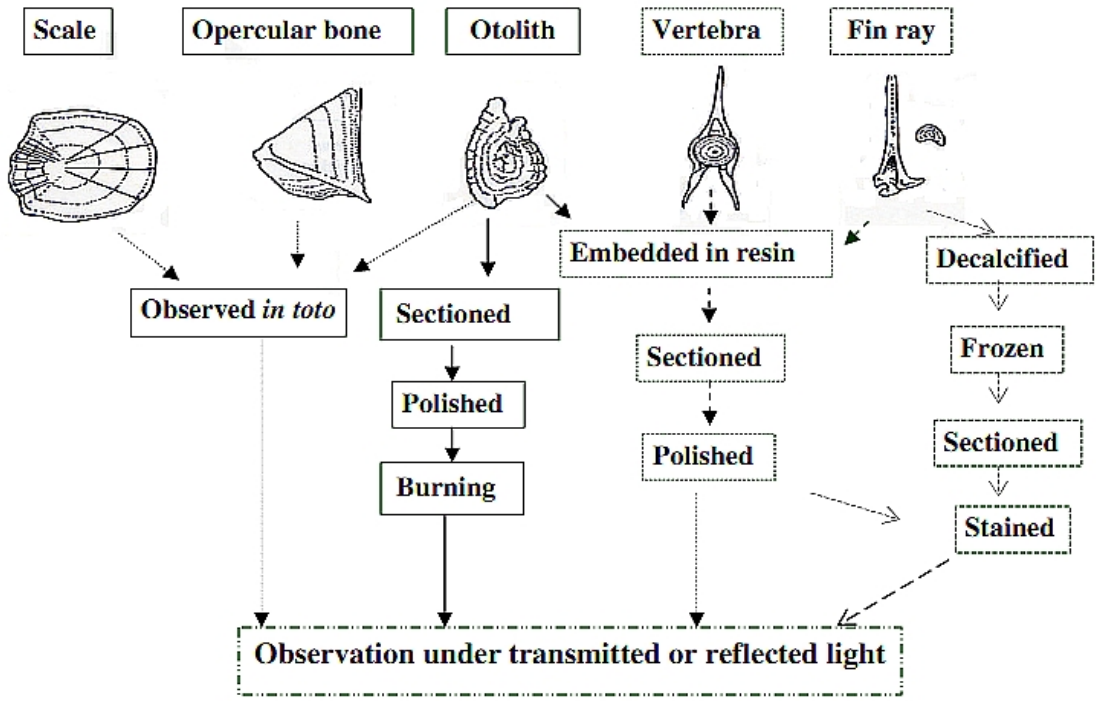


Fig. 2-3. Preparation procedure for hard structures for age determination in fish (Gaamour and Khemiri 2004).

Beamish and McFarlane 1987; Casselman 1990). In addition, unusual events; e. g. extreme water temperatures, injury or any stress that stop the growing of fish for a period of time; may cause false annuli on scales, leading to improper in age interpretation (Waston 1967; Schneider et al. 2000).

Otoliths are the calcium carbonate structures forming the inner ear of many vertebrates. There are three pairs of otoliths presented in fish which are lapilli, sagittae and astersci. Sagitta is the largest otolith and most used in age determination of fish (Secor et al. 1991). Unlike the scales, otoliths grow throughout the life of fish and are metabolically inert. Therefore, otoliths are likely unable to be absorbed or altered by the short-term changes in fish condition (Campana and Casselman 1993). The disadvantage of otolith ageing is that the otolith extraction requires killing the fish (Lux 1971).

According to Campana (2001), the process of estimating fish age incorporates two major sources of error, these are incomplete growth sequence error throughout the lifetime of the animal and error due to an element of subjectivity which may vary among age readers (Campana 2001). Ageing error can be of two forms: error that affects the accuracy (the closeness of age estimation to the true age), and error that affects the precision. Precision is defined as reproducibility of age determination; it describes the consistency of determinations among readers or hard structures used for age determinations (Beamish and Fournier 1981). Percentage agreement (PA) is one of the common and traditional techniques to compare the precision of age determinations. However, percent agreement techniques may not evaluate the degree of precision equally between short-lived with long-lived fish, hence, it fails to take into consideration the range of fish year-class as available to the fishery (Beamish and Fournier 1981; Chang 1982). Consequently, Beamish and Fournier (1981) introduced average percent error (APE), a method for comparing age precision as:

$$APE_j = \frac{1}{R_j}\sum_{i=1}^{R}\frac{|X_{ij} - X_j|}{X_j}$$

where R is repeat number of readings, X_{ij} is number of increments on the j-th otolith or scale read for the i-th time, and X_j is mean number of increments for the j-th otolith or scale.

Chang (1982) suggested coefficient of variation (CV) techniques which based on APE with the improvement by substitution the standard deviation for the absolute deviation from the mean age.

$$CV_j = \frac{\sqrt{\sum_{i=1}^{R} \frac{(X_{ij} - X_j)^2}{R-1}}}{X_j}$$

The APE and CV were then widely used in ageing research. According to Campana (2001), precision of age determination is not only influenced by age reader, but also by species and the nature ageing structure. Thereby, there are no specific value for APE and CV. However, the values of CV ≤ 10% and APE ≤ 7.6% are regularly used to evaluate the precision for age determination in vertebrate fishes.

Growth in fish can be estimated by direct observation, length-frequency distribution, back-calculation of length from hard structures, or by growth models from length-age data. The most common growth models are the von Bertalanffy, Gompertz, logistic, and Richards models (Hernandez-Llamas and Ratkowsky 2004; Akamine 2009; Quist et al. 2012).

The von Bertalanffy growth model

The von Bertalanffy growth function is one of the most popular growth models in fisheries science. The von Bertalanffy model allows for easy comparisons of growth among population or between sexes, is expressed as:

$$L_t = \mathrm{L}_\infty \left[1 - e^{-\mathrm{K}(t-\mathrm{t}_0)}\right],$$

where: L_t is length at age t in years, L_∞ is asymptotic length, K is growth coefficient, t_0 is theoretical age when length is equal to zero.

The Gompertz growth model

The Gompertz growth function is popularly used in describing the growth of larval and juvenile fish, expressed as:

$$L_t = \mathrm{L}_\infty \exp\left(-e^{-\mathrm{K}(t-\mathrm{t}_0)}\right),$$

The logistic growth model

The logistic growth function is often used to describe population growth rates, but it is also used to describe growth of individual fish.

$$L_t = \mathrm{L}_\infty [1 + e^{-\mathrm{K}(t-\mathrm{t}_0)}]^{-1},$$

The Richards growth model

The Richards growth function or generalized logistic is an extension of the logistic growth function, allows more flexible S-shaped curves. Richards curve requires one more parameter (r) than the logistic curve to generate asymmetry.

$$L_t = \mathrm{L}_\infty [1 + \mathrm{r}e^{-\mathrm{K}(t-\mathrm{t}_0)}]^{-1/r},$$

where r is the parameter that decides the shape of the growth curve.

According to Akamine (2009), Richards growth function also includes logistic, Gompertz, and von Bertalanffy growth function. If r=−1, approaching 0, and 1, Richards formula are same to von Bertalanffy, Gompertz, and logistic formulae, respectively.

2.3.2. Studies on feeding habits of fish

Studies on food and feeding habits of fish is important to understand the ecological role and position of the species in the food web of ecosystems. According to Saikia (2015), several challenges need to be addressed to obtain the accurate information about food and feeding habits of fish, such as: wide ranging in the inhabitation of fish (from marine to freshwater), especially in migrated fishes; morphological diversity in body size; ontogenetic shift in feeding habits; and the opportunistic feeding behavior in several fishes. Subsequently, the assessment of stomach content is necessary. Study of the diet based upon analysis of stomach contents is now standard practice in fish (Hyslop 1980). Hynes (1950) and Hyslop (1980) described the methods commonly used in studies of the stomach content of fish as the following:

The occurrence method

Recording number of fishes in which each food item occurs, this number may then be expressed as a percentage of all stomachs.

The numerical method

The number of individuals in each food category is recorded for all stomachs and the total is expressed as a percentage of the total individuals in all food categories.

The volumetric method

The total volume of a food category taken by the fish population is usually given as a percentage of the total volume of all stomach contents.

The gravimetric method

In this method, the total weight (can be dry weight or wet weight) of a food category is expressed as a percentage of the overall weight of stomach contents.

However, according to Pinkas et al. (1971), these traditional methods are insufficient in evaluating stomach contents in fish. For example, numerous small organisms overshadow the importance of a few large ones; differential digestive rates distort volumetric measurements; frequency of occurrence tabulations are sensitive to sampling error. Hence, Pinkas et el. (1971) developed an index of relative importance (IRI) to assist in evaluating the relationship of the various food items found in stomachs, the index is calculated as:

$$IRI_i = (\%N_i + \%V_i) \times \%F_i$$

the IRI is then expressed as percentage (with *i* is each prey item):

$$\%IRI_i = IRI_i \times 100/\sum IRI$$

where $\%N_i$ is numerical percentage; $\%F_i$ is frequency of occurrence percentage; $\%V_i$ is volumetric percentage for each prey item i (gravimetric percentage $\%W_i$ can also be used).

2.3.3. Water temperature, water salinity and normal development of eggs and larvae of fish

Fish live in the water; therefore, they are highly dependent to the water conditions. Several documents showed that survival, growth and development of fishes, especially in the early life stages are influenced by water temperature and

salinity (Tandler et al. 1995; Hart and Purser 1995; Boeuf and Payan 2001; Handeland et al. 2008). Water temperature can affect hatching rates, larval sizes at hatch, and larval survival, oxygen consumption, food intake, food conversion efficiency, and growth fish (Hart and Purser 1995; Hansen and Falk-Petersen 2001; Akatsu et al., 1983; Garcia-Lopez et al. 2004; Hernandez-Rubio and Figueroa-Lucero 2013). While, salinity affects egg fertilization and incubation, yolk-sac resorption, hatching rate and egg diameter, larval survival and growth (Holliday 1969; Lee and Menu 1981; Swanson 1996; Murashige et al. 1991; Boeuf and Payan 2001; Garcia-Lopez et al. 2004; Hernandez-Rubio and Figueroa-Lucero 2013).

In genus *Osmerus* fishes, most of studies on spawning migration of *O. mordax* occur only when the temperature reaches 3-4°C (Rupp 1959). Incubation times of *O. mordax* vary according to the water temperature and range from 9 days at 20°C to 32 days at 5°C. Hatching day of *O. mordax* is greater in range of 10°C to 15°C than at 5°C or 20°C. *O. mordax* larvae can be reared at the temperature of 15-20°C (Ayer et al. 2005). Whereas the salinity higher than 20 will cause the mortality for *O. mordax* embryos. At range of 2–20, larval growth rates increase significantly when salinities decrease (Ayer et al. 2005).

CHAPTER 3. AGE AND GROWTH OF PACIFIC RAINBOW SMELT *OSMERUS DENTEX* ESTIMATED FROM SCALES AND OTOLITHS IN FUNKA BAY AND THE YAMAZAKI RIVER, JAPAN

Abstract

For elucidation of the population dynamics and efficient use of the fisheries resource of Pacific rainbow smelt *Osmerus dentex*, I examined the appropriate age assessment method and growth trajectory of this species. Samples were collected with an otter trawl net along the sea-bottom in Funka Bay from October 2018 to September 2019 and a scoop net for spawners at the mouth of the Yamazaki River in late April to mid-May in 2019. Coefficient of variation and average percentage error of three readers by sagittal otolith reading (12.4% and 9.3%, respectively) were lower (better) than scale readings (15.1% and 11.4%). Percentage of agreement among three readers for otolith (41.2%) was higher than for scale (17.7%). Opaque margins in otoliths were found from March to August with the peak in April and May around the spawning period implying that the increments were formed annually. Maximum age was 6.8 years and the largest body size was 269 mm SL. *O. dentex* caught in this study area showed faster growth by growth performance index ϕ' than those in other areas, and this growth difference might be caused by the response to latitudinal effects, food availability, and photoperiod between areas.

3. 1. Introduction

Pacific rainbow smelt *Osmerus dentex* Steindachner & Kner 1870 is an anadromous fish species, and is distributed from the eastern part of the Korean Peninsula, Hokkaido, Sakhalin, Alaska, to the coast of the Russian Arctic Ocean (McAllister 1963). *O. dentex* is the only species of the genus *Osmerus* that occurs in Japan (Motomura 2020) and inhabits in and around Hokkaido Island (Horikawa and Kyushin 1987; Horikawa 1988; Inokuchi et al. 1997; Mutoh 2003a). *O. dentex* has the largest body-size in Osmeridae in Japan which includes six species, shishamo smelt *Spirinchus lanceolatus* Hikita 1913, Japanese surf smelt *Hypomesus japonicus* Brevoort 1856, wakasagi smelt *H. nipponensis* McAllister 1963, pond smelt *H. olidus* Pallas 1814, capelin *Mallotus villosus* Müller 1776, and Pacific rainbow smelt *O. dentex* (Motomura 2020).

In Funka Bay, spawning behavior, stock identification by morphological characters (numbers of fin rays, vertebrates, gill rakers, and pyloric caeca), egg size and fecundity, oocyte development and temporal and spatial distribution of *Osmerus eperlanus mordax* have been examined (Horikawa and Kyushin 1987; Horikawa 1988; Inokuchi et al. 1997), which is a synonym of *O. dentex* (Kawai 2020). In addition, in the Yamazaki River in Yakumo Town bordering Funka Bay, *O. dentex* migrates up the river from late April to mid-May for spawning. In this species, the gonads are asymmetrical, the left side one is larger than the right side, and the fecundity range is 17,500-211,600 (Horikawa 1988). This species supports recreational fishing in the Yamazaki River and as a bycatch in small set nets for Japanese surf smelt in the coastal area of Funka Bay, and as a result, no catch data is available (Inokuchi et al. 1997). Ecological features, especially the growth trajectory of this species have not been researched. Estimation of age and growth parameters is necessary to elucidate the population dynamics of this species, for the conservation and efficient utilization of this resource. The goals of this study: 1) to compare the reliability between ageing *O. dentex* using sagittal otolith and scale methods, and 2) to describe the growth features of *O. dentex* collected in Funka Bay

and at the mouth part of the Yamazaki River.

3.2. Materials and Methods

Samples of *O. dentex* were collected with an otter trawl net along the sea-bottom from the T/S *Ushio-maru* of Hokkaido University, Faculty of Fisheries in Funka Bay from October 2018 to September of 2019 (Fig. 3-1, Table 3-1). Scoop net sampling for spawners was carried out at the mouth of the Yamazaki River in late April to mid-May in 2019. All specimens were immediately refrigerated or frozen and brought back to the laboratory for frozen storage.

In the laboratory, specimens were thawed, and total length (TL) and standard length (SL) were measured to the nearest 1 mm. Body weight (BW) and gonad weight were weighed to the nearest 0.1 g and sex, based on the morphology of the gonads was recorded. The condition factor (CF) of fish was calculated following Sekigawa et al. (2002) as:

$$CF = (BW-GW-SCW)/SL^3 \cdot 10^5$$

Where CF is the condition factor, BW is body weight (g), GW is gonads weight (g), SCW is the stomach content weight (g), SL is standard length (mm). The student's *t*-test was carried out to analyze the significant difference between monthly mean condition factor of fish between male and female. The gonadosomatic index (GSI) was calculated using the following formula:

$$GSI = 100 \times GW/(BW-GW)$$

Sagittal otoliths were removed from the head and stored using microplates in a dry condition. Three to five scales were removed from the median section of the body adjacent to the lateral line with tweezers, attached to glass slides and stored dry for later analysis. To compare the results with those of previous papers in which fork length (FL) of *O. dentex* was used, FL and SL were measured on 30 additional individuals.

The number of translucent-zone edges on otoliths between the focus and the outermost edge was counted under a binocular dissecting microscope at

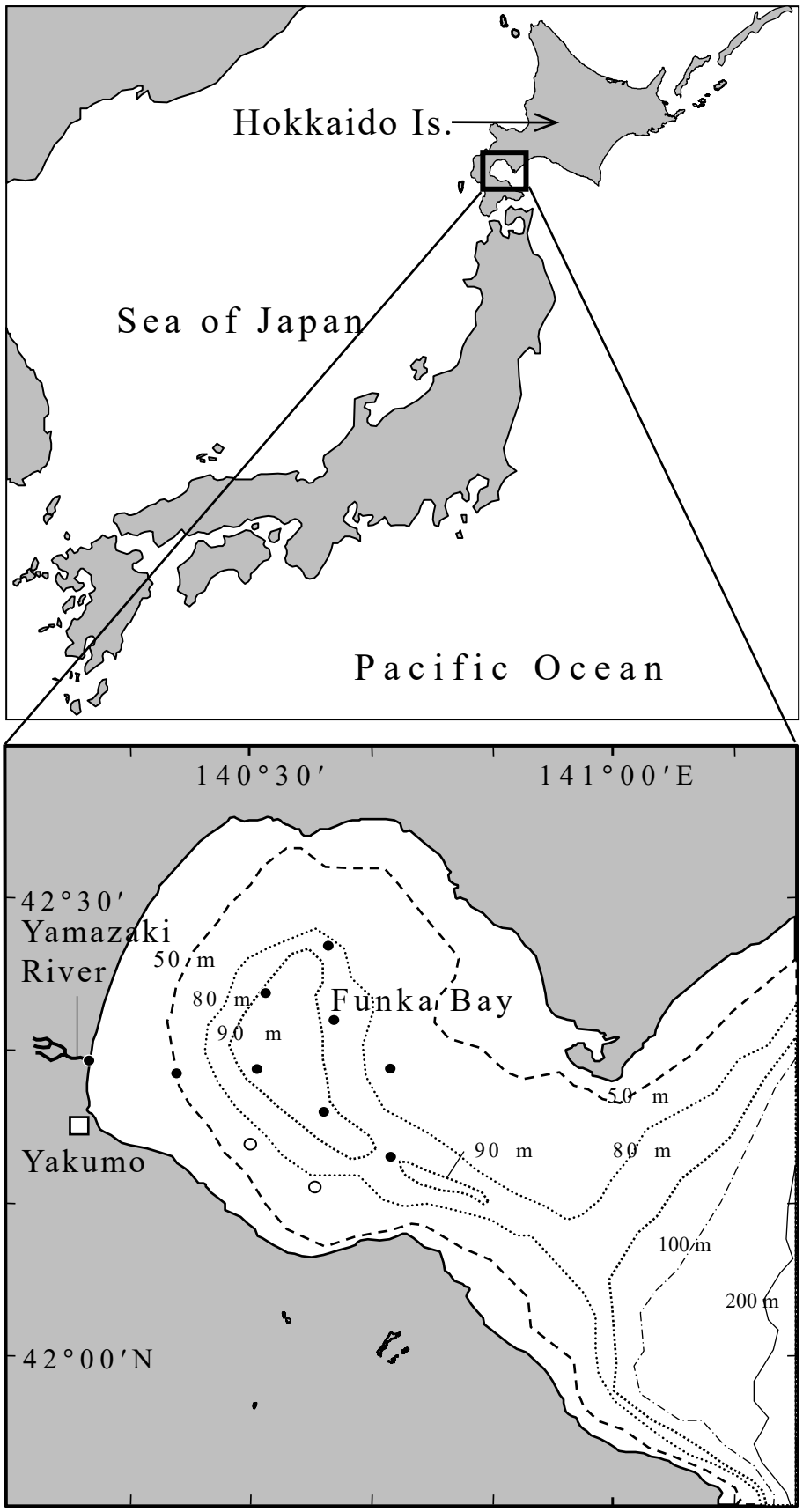


Fig. 3-1. Map of sampling stations for *O. dentex* in Funka Bay with bottom isobaths and the mouth part of the Yamazaki River. Solid and open circles show stations where *O. dentex* were sampled and not sampled, respectively.

Table 3-1. List of samples for Pacific rainbow smelt *Osmerus dentex* in this study

Sampling date	Sampling gear	Number of samples	Range of standard length (mm)	Location
October 3-5, 2018	Otter trawl	52	101-269	Funka Bay
November 13-14, 2018	Otter trawl	53	116-266	Funka Bay
January 13, 2019	Otter trawl	5	132-212	Funka Bay
February 11-12, 2019	Otter trawl	3	99-203	Funka Bay
March 17, 2019	Otter trawl	7	114-170	Funka Bay
April 16-17, 2019	Otter trawl	11	115-232	Funka Bay
April 29, 2019	Scoop net	26	182-243	Yamazaki River
May 3, 2019	Scoop net	44	158-256	Yamazaki River
May 8, 2019	Scoop net	30	160-260	Yamazaki River
May 15, 2019	Scoop net	31	158-264	Yamazaki River
May 15-16, 2019	Otter trawl	3	162-242	Funka Bay
August 25-27, 2019	Otter trawl	10	144-252	Funka Bay
September 29, 2019	Otter trawl	15	118-266	Funka Bay

8-40X magnification with reflected light (Fig. 3-2a). The outward growth lines converge and allow more light to pass through on scales (Walsh et al. 2008; Fig. 3-2b), so I and other two researchers counted number of increments on scales under the same microscope at 8-40X magnification with transmitted light.

Otolith and scale readings were performed by three independent readers without access to any data attributions (sampling date, body weight, or standard length). The precision of the reading was assessed using the average percentage error (APE; Beamish and Fournier 1981) and coefficient of variation (CV; Chang 1982; Campana 2001):

$$APE_j = \frac{1}{R_j}\sum_{i=1}^{R}\frac{|X_{ij}-X_j|}{X_j},\ CV_j = \frac{\sqrt{\sum_{i=1}^{R}\frac{(X_{ij}-X_j)^2}{R-1}}}{X_j},$$

where R is repeat number of readings, X_{ij} is number of increments on the j-th otolith or scale read for the i-th time, and X_j is mean number of increments for the j-th otolith or scale. We also used percentage of agreement (PA) for the assessment of precision, which was the percentage of structures that are aged the same by the three different readers.

Parameters of the following four growth equations were estimated using the least-squares method:

$$\text{logistic:}\quad SL_t = \mathrm{SL}_\infty[1+e^{-\mathrm{K}(t-\mathrm{t}_0)}]^{-1},$$

$$\text{Gompertz:}\quad SL_t = \mathrm{SL}_\infty \exp\left(-e^{-\mathrm{K}(t-\mathrm{t}_0)}\right),$$

$$\text{von Bertalanffy:}\quad SL_t = \mathrm{SL}_\infty\left[1-e^{-\mathrm{K}(t-\mathrm{t}_0)}\right],$$

$$\text{and Richard:}\quad SL_t = \mathrm{SL}_\infty[1+\mathrm{r}e^{-\mathrm{K}(t-\mathrm{t}_0)}]^{-1/\mathrm{r}}.$$

where: SL_t is standard length at age t in years, SL_∞ is asymptotic length, K is growth coefficient, t_0 is theoretical age when length is equal to zero, and r is equation parameter for Richards formula. If r=−1, approaching 0, and 1, Richards formula is effectively the same as the von Bertalanffy, Gompertz, and logistic formulae, respectively. The best growth formula was selected from the

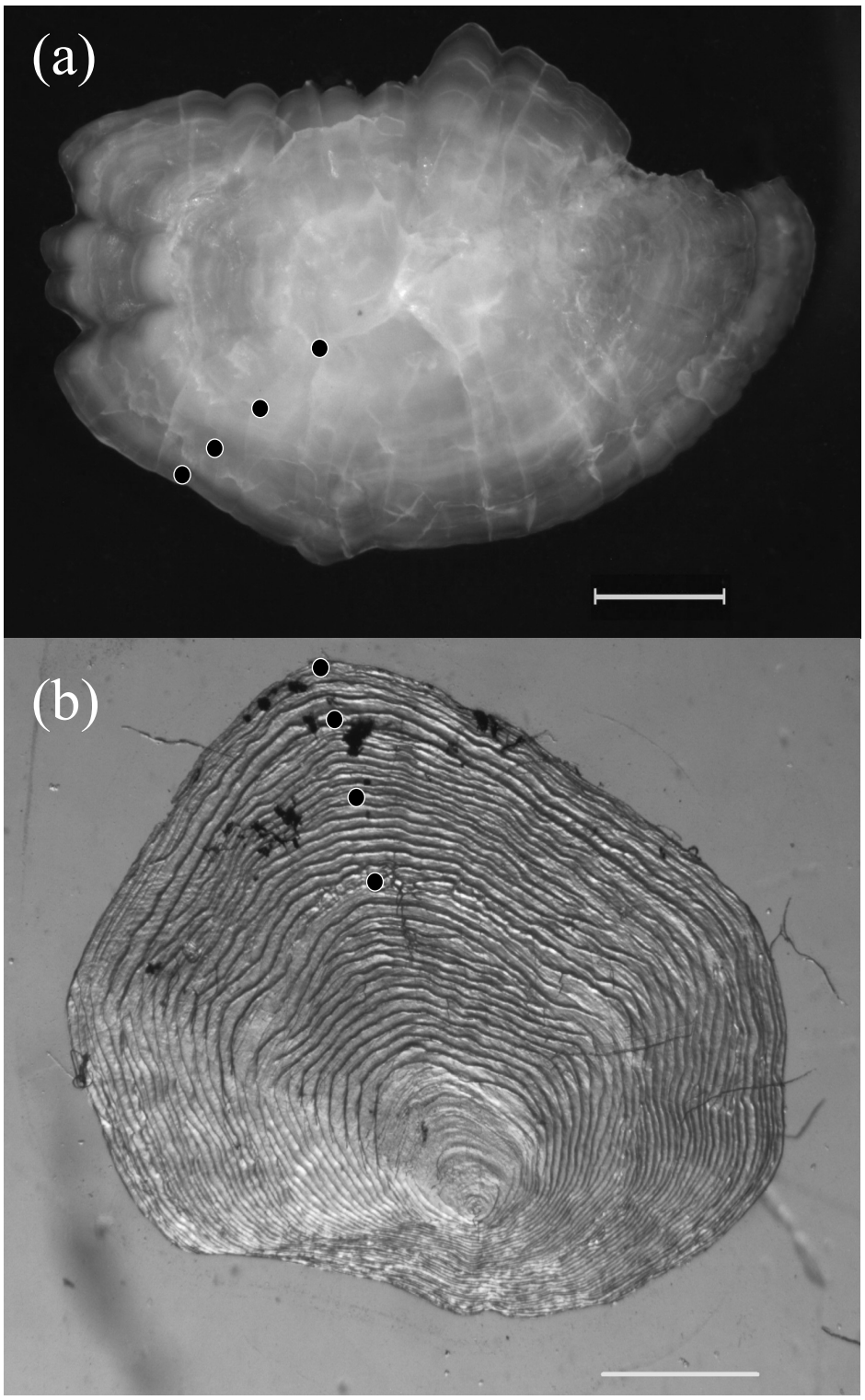


Fig. 3-2. A sagittal otolith (a) and a scale (b) from the same individual of *O. dentex* collected in May 2019. Solid circles show the increments (translucent edges of the otolith and outward growth lines that converged and allowed more light to pass through of the scale). Scale bars show 1 mm.

differences of AIC and MAIC (ΔAIC=AIC−$MAIC$) where MAIC was the minimum AIC.

$$AIC = 2k - 2\ln\hat{L}$$

where k is the number of estimated parameters in the formula and $\hat{L}$ is the maximum value of the likelihood for the formula. Goodness of fit between these growth formulae was also judged by r^2.

Hatching date of this population was assumed as May 1 because *O. dentex* migrates to the Yamazaki River for spawning from late April to mid-May. Three parameters between sexes were statistically tested by the likelihood method of Kimura (1980). Comparison of growth speed was evaluated using the growth performance index ϕ' (Munro and Pauly 1983; Pauly and Munro 1984) between *O. dentex* in this study and previous studies on *Osmerus mordax dentex* (synonym of *O. dentex*) in Norton Sound and Southeastern Chukchi Sea (Alaska, USA; Wolotira et al. 1979) and Beaufort Sea (Alaska; Haldorson and Craig 1984).

$$\phi' = \log K + 2 \log L_\infty$$

where K is growth coefficient and L_∞ in mm is asymptotic length of von Bertalanffy. To calculate ϕ' using fork length (FL), a regression line between FL and SL was estimated from 30 individuals of *O. dentex*.

3. 3. Results

3.3.1. Size frequently distributions

A total of 290 *O. dentex* were collected from Funka Bay and the Yamazaki River (Table 3-1). Of these fishes, 146 were males, 117 were females, and 27 were immature with sex undifferentiated. Body size ranges were 99–269 mm in standard length (Fig. 3-3) and 7.4–212.3 g in body weight.

3.3.2. Allometric relationships and condition factor

Relationships between total length (FL) and standard length (SL) of *O. dentex* with both sexes combined was expressed by the following equation: FL=1.10SL–5.52

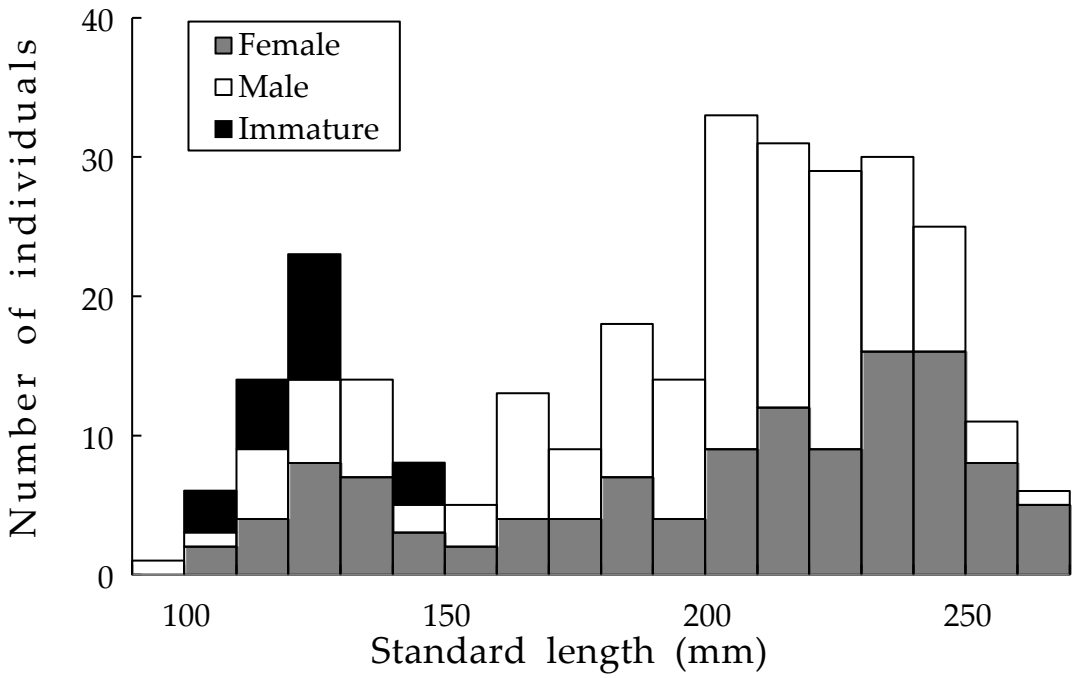


Fig. 3-3. Length frequency distribution of *O. dentex* for growth analyses during study period.

(r^2=0.99, P<0.001, n=30; Fig. 3-4a), and the intercept was significantly different from 0 (P<0.001). Relationships between SL and body weight (BW; sexes combined) was expressed by the following equation: $BW=10^{-6}SL^{3.39}$ (r^2=0.98, P<0.001; Fig. 3-4b).

Mean condition factor of *O. dentex* in Funka Bay and the Yamazaki River mouth ranged from 0.75 to 1.01 in male and 0.59 to 0.98 in female. A slightly decreasing in condition factor, especially in female, before spawning season of fish (February to March) was recorded. In April and May, mean condition factors of male *O. dentex* were recorded significantly higher than that of female (t-test, P<0.005; Fig. 3-5).

3.3.3. Comparison of the number of increment readings between otoliths and scales

Differences in number of increments among three readers were evaluated based on the coefficient of variation (CV), average percentage of error (APE), and percentage of agreement (PA). Mean CV and APE of three readers by otolith reading were 12.4% and 9.3%, respectively, and those were lower (better) than those by scale reading (15.1% and 11.4%, respectively; Table 3-2). PA among the three readers for otolith (41.2%) was higher (better) than that for scale reading (17.7%).

The first author compared the number of otolith and scale increments on 190 individuals (Fig. 3-6). The slope of the regression equation between otolith and scale readings was not significantly different from 1 (P=0.30, t-test). Mean number of increments counted by the otolith method was 3.44 ± 1.30 (± standard deviation), and that was significantly higher than by the scale method (3.32 ± 1.22; P < 0.001, paired t-test). The number of scale increments was frequently less than otolith increments, when the scale increments ranged from 4 to 6 it ranged from 5 to 6 for otolith increments.

3.3.4. Seasonal change in opaque-margin formation on otolith

Opaque margins of *O. dentex* otoliths were observed from March to November, with a peak from April to May (100%; Fig. 3-7). Translucent margins appeared from August to March, and all specimens had translucent margins in January and February.

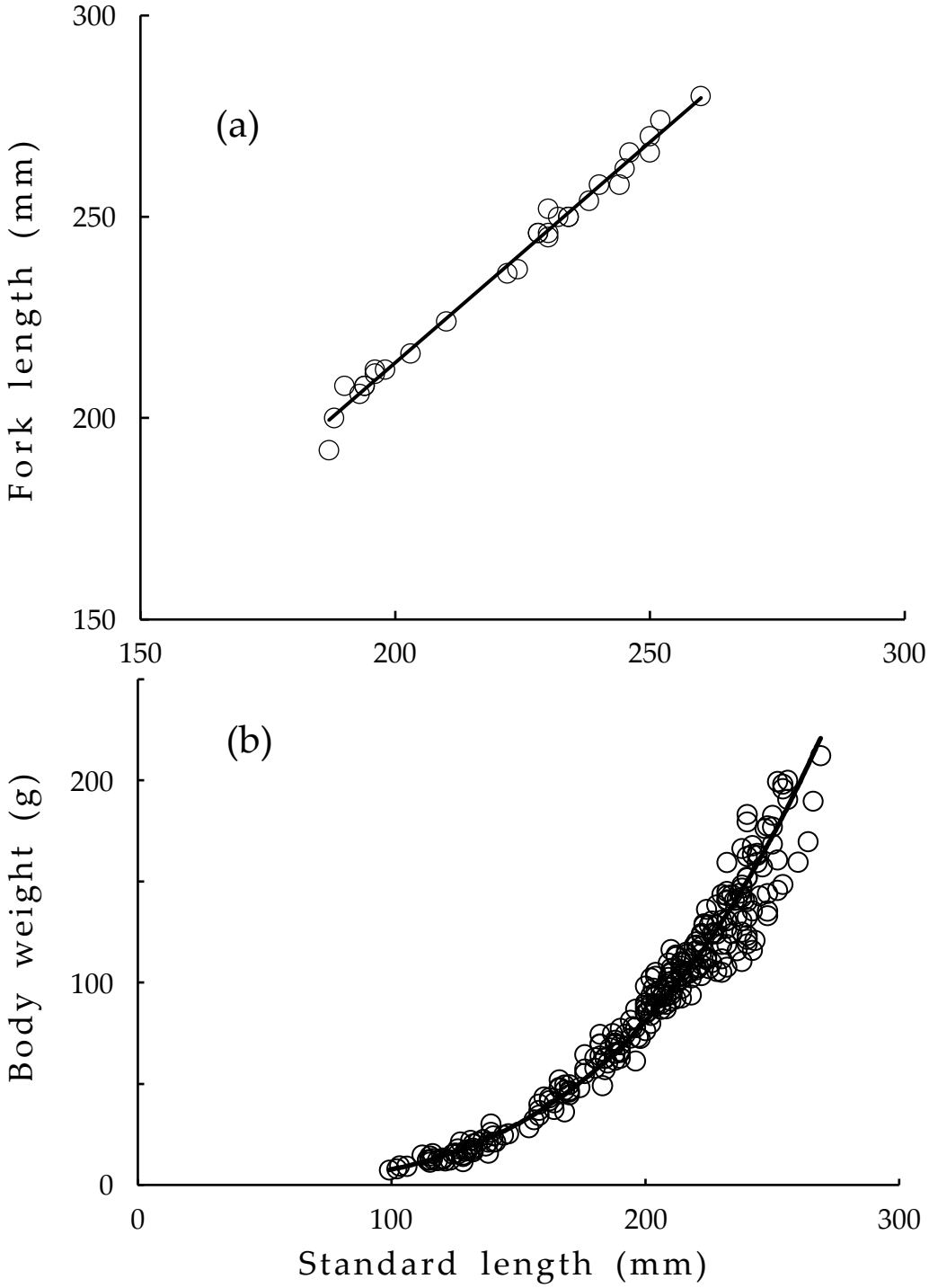


Fig. 3-4. Relationship between fork length and standard length (a), and standard length and body weight (b) of *O. dentex* in Funka Bay and the mouth part of the Yamazaki River.

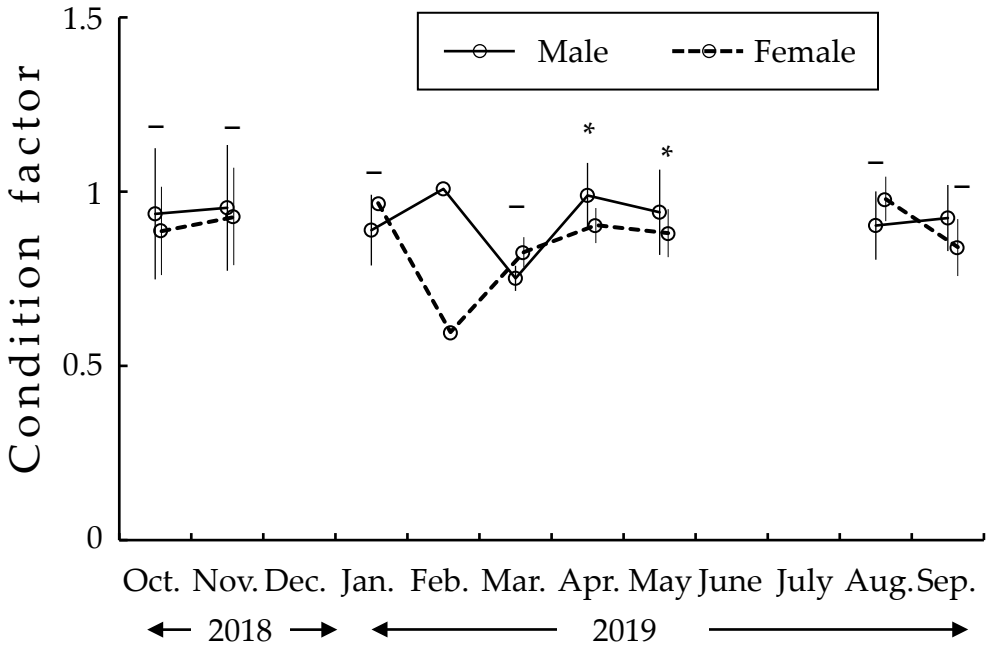


Fig. 3-5. Mean condition factor of male and female *O. dentex* in Funka Bay and the mouth part of the Yamazaki River.

Table 3-2. Age precision between otolith and scale reading among independent three readers

	Scale	Otolith
Percentage of agreement (PA; %)	17.7	41.2
Coefficient of variation (CV; %)	15.1	12.4
Average percentage of error (APE; %)	11.4	9.3

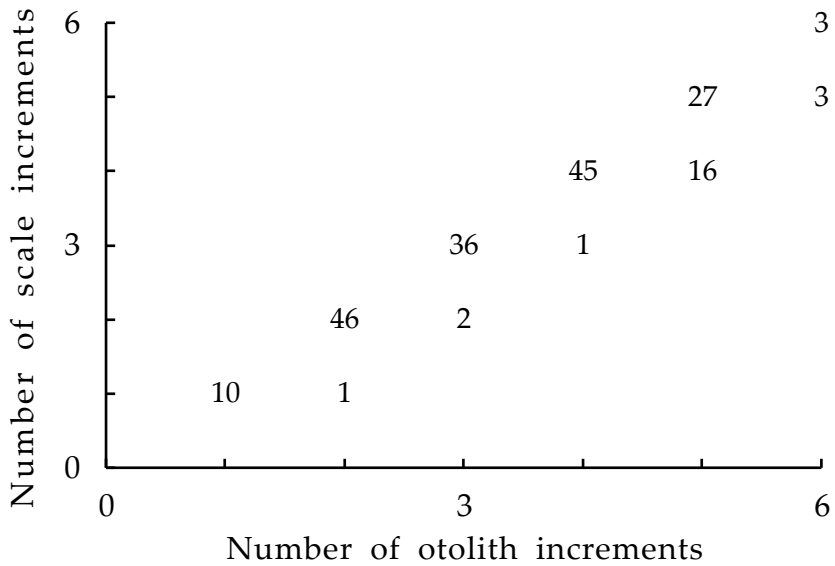


Fig. 3-6. Comparison of annulus counts between the sagittal otolith method and the scale method. Numerals show the number of individuals analyzed.

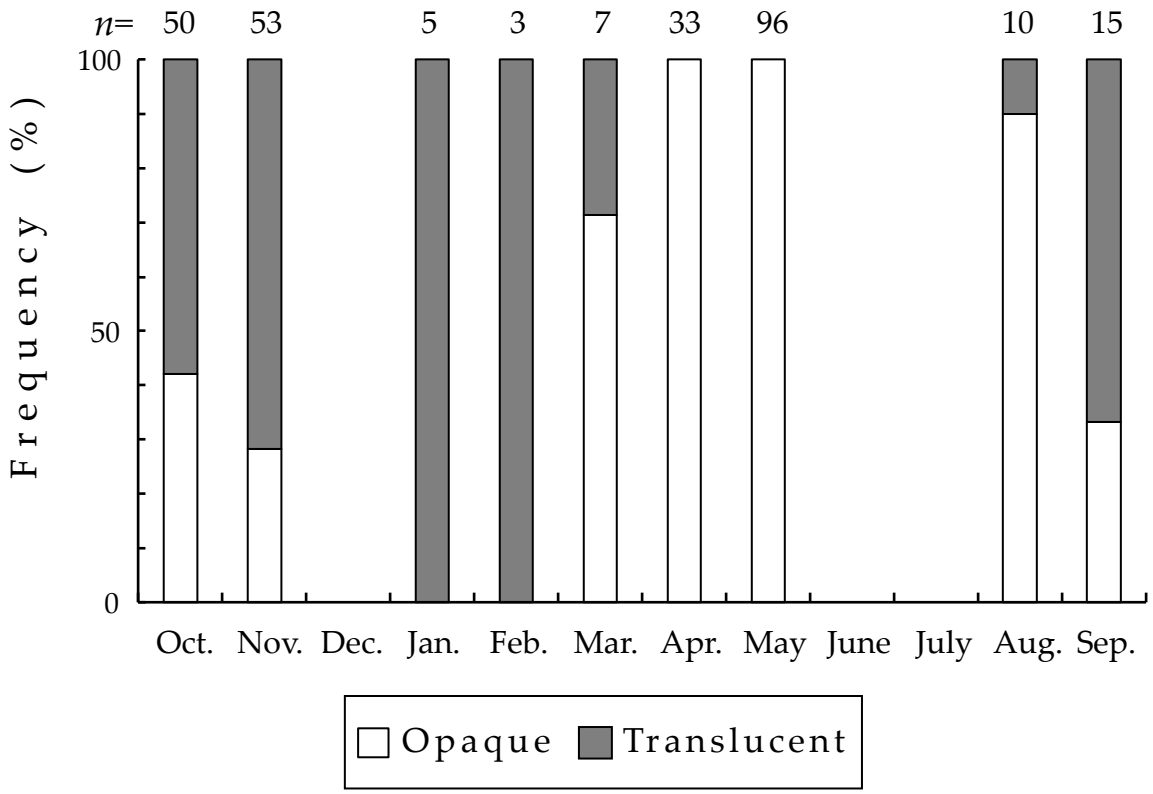


Fig. 3-7. Monthly change in percentage occurrence of opaque and translucent edges in sagittal otolith of *O. dentex*.

3.3.5. Seasonal change in gonadosomatic index

Female *O. dentex* ≥ 148 mm SL with > 3.0 GSI is matured in Funka Bay in February (Inokuchi et al. 1997). We treated females with ≥ 148 mm SL as adult female in this study. Minimum matured body size of male *O. dentex* has not been clarified, I plot the relationship between SL and GSI obtained before and in spawning season from November to May (Fig. 3-8). Because males of *O. dentex* ≥ 158 mm SL exclusive of an individual collected in May (162 mm SL and 0.77 GSI) were divided from smaller-sized ones at 1.9 in GSI, I treated males with ≥ 158 mm SL as adult male.

The highest mean GSI of adult male *O. dentex* was recorded in May (5.82 ± 2.46) and the lowest one in October (1.70 ± 1.25; Fig. 3-9) in samples with ≥ 7 individuals. The highest mean GSI of adult female *O. dentex* was recorded in May (27.09 ± 11.95) and the lowest one in August (0.59 ± 0.21).

3.3.6. Growth curve estimated from data at catch

A total of 290 *O. dentex* were collected, 273 otoliths extracted from the fish were used to estimate the growth curve, while 17 otoliths were not used to estimate the growth equation because they were damaged or their increments were unclear. The maximum age and body size of *O. dentex* by otolith reading were 6.8 years and 269 mm SL (289 mm FL and 310 mm TL). There were no significant differences between all three parameters in the two growth equations of von Bertalanffy for sex calculated separately and the growth equation was combined into one (likelihood ratio test; Kimura (1980): χ^2=4.23, *d.f.*=3, *P*=0.24). The growth parameters were computed for pooled females, males, and immature (undifferentiated) specimens using individual length-at-age data. The logistic, Gompertz, von Bertalanffy, and Richards growth equations estimated from data of SL and age using otolith were as the following (all: *n*=252, *P*<0.001; Fig. 3-10):

logistic: $SL_t = 252.63[1 + e^{-0.68(t-1.08)}]^{-1}$, ($r^2$=0.858, ΔAIC=+0.08)

Gompertz: $SL_t = 260.22\exp\left(-e^{-0.51(t-1.64)}\right)$, ($r^2$=0.858, ΔAIC=0)

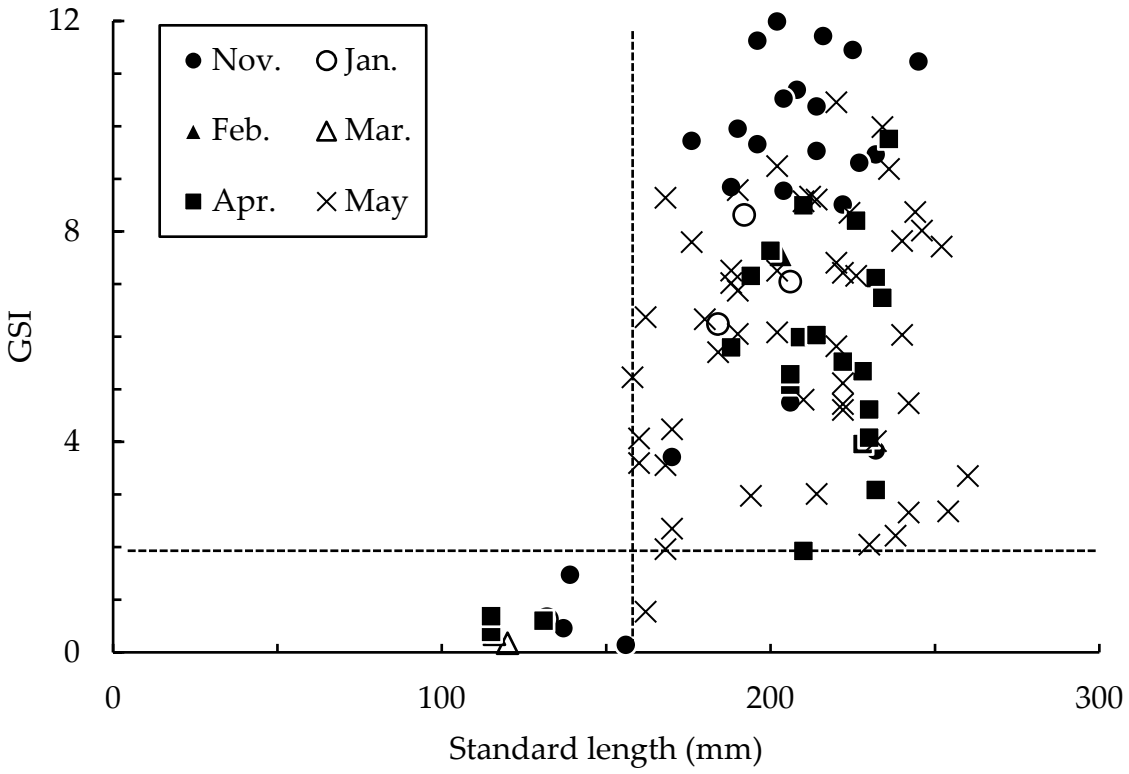


Fig. 3-8. Relationship between gonadosomatic index (GSI) and SL of male *O. dentex* collected from November to May in Funka Bay and the Yamazaki River.

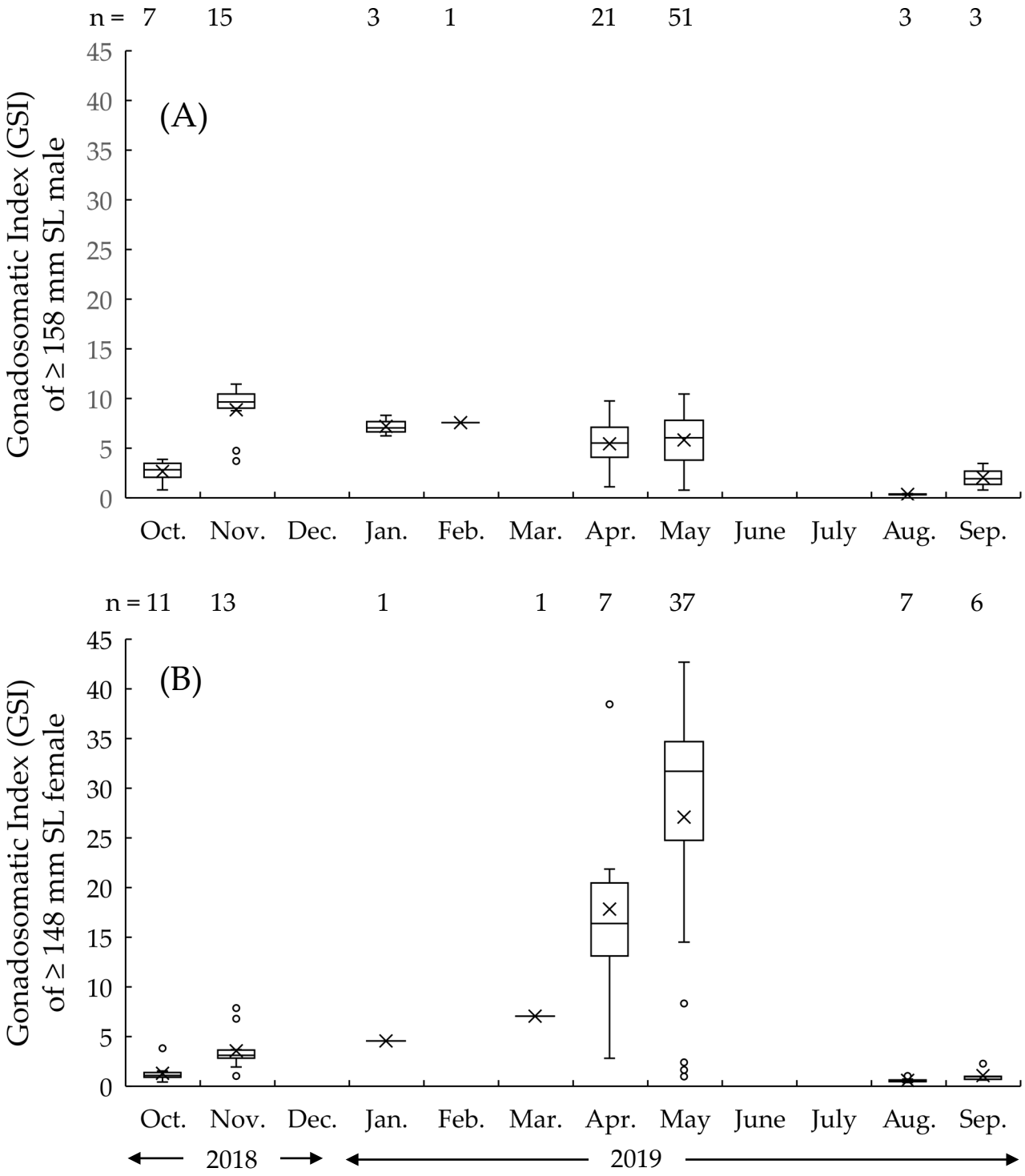


Fig. 3-9. Seasonal changes in mean gonadosomatic index (GSI) of ≥ 158 mm SL male and ≥ 148 mm SL female *O. dentex* in Funka Bay and the Yamazaki river

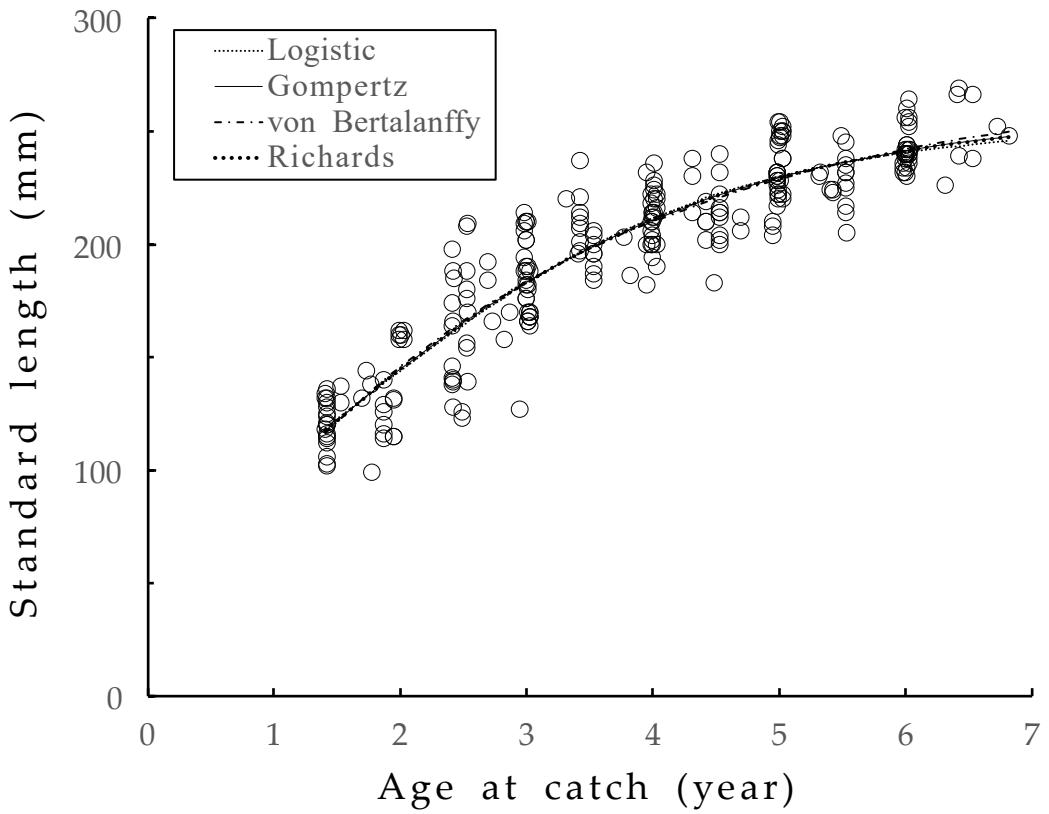


Fig. 3-10. The logistic, Gompertz, von Bertalanffy, and Richards growth curve based on age and standard-length data at catch.

von Bertalanffy: $SL_t = 273.82\left[1 - e^{-0.35(t+0.18)}\right]$, ($r^2$=0.858, ΔAIC=+0.13)

Richards: $SL_t = 259.31[1 + 0.10e^{-0.53(t-1.04)}]^{-1/0.10}$, ($r^2$=0.858, ΔAIC=+2.00).

Growth performance indices (ϕ') were calculated as 4.55 by direct estimation of von Bertalanffy using TL measured and as 4.48 using the FL regression formula in Fig. 3-4a (Table 3-3).

3.4. Discussions

We found that the otolith increment pattern is more reliable for age assessment than using the scales in *O. dentex* in Funka Bay and the Yamazaki River. Hard structures such as scales, otoliths, spines, cleithra, and vertebrae are widely used in age determination of fish. The process of estimating fish age incorporates two major sources of error, these are incomplete growth sequence error throughout the lifetime of the animal and error due to an element of subjectivity which may vary among age readers (Campana 2001). The error between readers can be estimated by determining the variability of the age assessment results for common samples. According to McBride (2015), the most commonly used approach to evaluate age error is indices of precision which include percentage of agreement (PA), average percentage error (APE), and coefficient of variation (CV). The threshold values of CV ≤ 10% and APE ≤ 7.6% are regularly used to evaluate the precision for age determination in vertebrate fishes (Campana 2001). In this study, CVs and APEs of the three readers were 12.4% and 9.3% for otolith reading, and 15.1% and 11.4% for scale reading, respectively (Table 3-2), and these index-values of *O. dentex* were slightly higher than the threshold values. Additionally, O'Malley et al. (2017) stated that when the true age of fish is unknown, structure which enable a higher level of agreement between readers are preferrable, results from the present study showed that the percentage of agreement (PA) of the three readers on otolith reading (41.2%) was higher than of scale reading (17.7%). In comparison between the otolith reading and scale reading, otoliths might be a more reliable increment structure of *O. dentex* than those of scales. This difference might be due to under-counting of the

Table 3-3. Comparisons between maximum age (year), maximum body length (L_{max}; mm) and von Bertalanffy growth parameters of Pacific rainbow smelt *O. dentex* in this study and previous studies

Location	Max. Age	L_{max}	L_{∞_FL}	L_{∞_TL}	K	t_0	ϕ'	Year	Measurement	Sex	Reference
Olyutorsky, RU	10	360						2016	Fork length	-	Datsky (2017)
Mackenzie Bay in Beaufort Sea, CA	8	320						1975	Fork length	-	Poulin (1976)
Beaufort Sea, AK, USA	-	310	325		0.224	0.5	4.37*	1984	Fork length	Pooled	Haldorson and Craig (1984)
Norton Sound, AK, USA	9	360		216	0.24	0.01	4.05*	1976	Total length	Male	Wolotira et al. (1979)
Norton Sound, AK, USA	9	360		247	0.21	0.04	4.11*	1976	Total length	Female	Wolotira et al. (1979)
Southeastern Chukchi Sea	9	360		379	0.11	0.08	4.20*	1976	Total length	Male	Wolotira et al. (1979)
Southeastern Chukchi Sea	9	360		296	0.18	0.06	4.20*	1976	Total length	Female	Wolotira et al. (1979)
Funka Bay, JP	6.8	289	297		0.342	−0.12	4.48**	2018-2019	Fork length	Pooled	This study in FL
Funka Bay, JP	6.8	310		314	0.362	−0.16	4.55	2018-2019	Total length	Pooled	This study in TL

* Growth performance index ϕ' was calculated from L_∞ and K values by authors,

** ϕ' was calculated from SLs with FL=1.10 SL – 5.52 shown in Fig. 3-4a.

increments close to the scale margins (Figs. 3-2 and 3-6). Low reliability of slightly higher CV and APE for otolith reading in *O. dentex* than threshold values by Campana (2001) might be due to the low contrast difference between translucent and opaque zones in the otoliths (Fig. 3-2).

Several studies about age estimation of *O. mordax* have been conducted in North America by using hard structures of fish such as scales (McKenzie 1958; Bailey 1964; Elzey et al. 2010; O'Malley et al. 2017), fin rays (Walsh et al. 2008), and otoliths (Sirois et al. 1998; Curry et al. 2004; Walsh et al. 2008; Mrnak 2016; O'Malley et al. 2017). Elzey et al. (2010) reported age estimation of *O. mordax* using scales for the reason of the short life span causing outer annuli of *O. mordax* to be easily visible and more precise than that using otoliths. In contrast, age determination using scales of *O. dentex* had a larger bias than that using otoliths in this study (low PA, high CV, and high APE; Table 3-2). Several authors gave evidence to show that scale ageing might lead to underestimation the age of fish, especially when growth becomes asymptotic (Table 3-4). A similar trend was observed in this study (Fig. 3-6): when the age of *O. dentex* was higher than 4, the number of increments counted on scales was less than those on otoliths. A possible explanation for this result could be due to the resorption of scales by anadromous fish especially during spawning events which may lead to a less reliable estimation of age (Muir et al. 2008; O'Malley et al. 2017; Copeland et al. 2018). Accordingly, increment counts from otolith reading was selected for use in estimation of age of *O. dentex* in this study.

Because translucent and opaque zones in otoliths of *O. dentex* were found to form alternately once a year (Fig. 3-7), the increments were judged to be annual rings. Understanding the formation process of hard structures is necessary to be able to interpret age of fish from hard structures. According to Katayama et al. (2010), otolith structures of almost all species of fish are formed seasonally. Fitch (1951) used the high percentage of fishes with opaque margins to define the formation of annual rings in Pacific mackerel *Scomber japonicus*. A similar method

Table 3-4. Examples of ageing error using scales method (modified from Beamish and McFarlane 1987; Hamada 1961; Ashford et al. 2001; Beckman 2002; Horka et al. 2010; Tyszko and Pritt 2017)

Species	Desciption	References
Salvelinus namaycus	Scale growth slows down at maturity while otoliths continue to grow in relation to length increases.	Simard and Magnin (1972)*
S. fontinalis	Scale age was generally less than ototlith age and could underestimate ages by 40%.	Dutil and Power (1977)*
Coregonus albula	Scales ages are mostly lower than otolith ages with disagreement at all age levels.	Aass (1972)*
Prosopium cylindraceum	Scales underestimated the age of older fish	Jessop (1972)*
Coregonus clupeaformis	Otolith cross-section ages up to 35 yr older than previously recorded maximum age using scales	Power (1978)*
C. clupeaformis	Fin-ray ages were older than scales ages for slower growing fish	Mills and Beamish (1980)*
C. clupeaformis	Scales underestimated the age of western Labrador lake whitefish, discrepancies occur from age 4 or 5.	Barnes and Power (1984)*
Thymallus arcticus	Scales ages undereastimated the ages of old fish.	Craig and Poulin (1975)*
T. arcticus	Ages determined from scales may underestimate the true age	Sikstrom (1983)*
Exos masquinongy	Fish older than 9 could not be aged from scales.	Harrison and Hadley (1979)*
Rutilus rutilus	Scales ages undereastimate older ages	Hansen (1978)*
Catostomus commersoni	Scales age are unreliable beyond the age of maturity	Beamish (1973)*
C. commersoni	Tagging studies confirmed that scale age substantially underestimates true age	Beamish and McFarlane (1983)*
Microteprus salmoides	Scales are likely to underestimate true ages of older fish.	Maraldo and MacCrimmon (1979)*
Perca flavescens	For older fish cleithra provides more reliable ages than scales	Schmitt and Hubert (1981)*
Stizostedion vitreum vitreum	Scale method underestimates ages of older fish in unexploited populations	Campell and Balaluk (1979)*
S. vitreum vitreum	Otolith or pectoral fin-ray ageing methods should be used as an occasional check for the scale ages.	Belanger and Hogler (1982)*
Aplodinotus grunniens	Oldest fish underestimated by scale method, scales only 61% reliable for ageing this species	Goeman et al. (1984)*
Gadus macrocephalus	Length-frequency analysis indicate more older fish, slower growth, and greater longervity than scale method	Foucher et al. (1984)*

Species	Desciption	References
Anoplopoma fimbria	Ages from otolith sections from sablefish in the commercial fishery range from 8-45 yr compare to 5-10 yr by scale method.	Beamish and Chilton (1982)*
Ophiodon elongatus	Scale age unreliable for fish shortly after the of maturity. Scales age can be only 1/2 of true age.	Beamish and Chilton (1977)*
Hypomesus sakhalinus (synonym of H. olidus)	Annulus may be not always formed on the scales of *H. sakhalinus*. The circuli on the scale showed irregular form in the region of the margin. The scales is not an adequate criterion for the age of *H. sakhalinus*.	Hamada (1961)
Dissoslicliirs elcginoides	Ages estimated using scales were significantly less than those estimated using otoliths. Scales ageing is more bias than otoliths.	Ashford et al. (2001)
Etheostoma caeruleum	Scales underestimated age compared to otoliths. Scale showed no clear pattern of annulus formation.	Beckman (2002)
Thymallus thymallus	Age assigned from scales underestimated the tag-recapture assigned age by as much as 3 years. Accuracy of fish ageing by scales was highest in 1 and 2 year-old fish but decreased in older fish.	Horka et al. (2010)
Micropterus salmoides	Otolith-derived age estimates were more precise; scale-derived age estimates showed significant positive bias for fish younger than age 6 and significant negative bias for fish older than age 6.	Tyszko and Pritt (2017)

*: described by Beamish and McFarlane (1987).

has been applied to determine of oriental sillago *Sillago aeolus* (Rahman and Tachihara 2005), several flatfishes (Katayama et al. 2010), and pike conger *Muraenesox cinereus* (Watari et al. 2013). The formation of opaque rings/zones in fish has been associated to various factors such as water temperature, feeding, and especially the spawning period (Rahman and Tachihara 2005; Watari et al. 2013). High percentage of opaque margins of *O. dentex* was found from March to August with the peak in April and May around the spawning period in Funka Bay and the Yamazaki River (Fig. 3-7).

Previous studies showed that maximum age of *O. dentex* ranged from 8–10 years old (Poulin 1976; Wolotira et al. 1979; Datsky 2017; Table 3.3). The maximum age and body size of *O. dentex* in Funka Bay and the Yamazaki River of 6.8 years and 269 mm SL (289 mm FL and 310 mm TL) were generally lower than those in the other studies. Growth coefficients (K) in von Bertalanffy growth curves obtained from this study (0.342 and 0.362 by FL and TL, respectively) were higher than that of *O. dentex* collected in the Beaufort Sea off Alaska in the Arctic Ocean (0.224 by FL; Haldorson and Craig 1984; Fig. 3-11) and Norton Sound in the Bering Sea (0.24 and 0.21 by TL) and southeastern Chukchi Sea in the Arctic Ocean (0.11 and 0.18 by TL; Wolotira et al. 1979; Table 3-3). Asymptotic length (L_∞) obtained from this study (297 mm FL and 314 mm TL) was smaller than those in the Beaufort Sea (325 mm FL) and of males in the Chukchi Sea (379 mm TL) but not in Norton Sound (216 mm FL and 247 mm TL) and of females in the Chukchi Sea (296 mm TL). Several fishes distributed at higher latitudes show larger maximum size (L_∞) and age together with low growth coefficient (K) (Trip et al. 2014). Funka Bay is located in a more southern latitude (ca. 42.3°N) than Norton Sound (ca. 64.6°N) and Beaufort Sea (ca. 70.5°N). But differences in K and L_∞ of *O. dentex* could not be explained directly by the latitudes of the three populations. The growth performance index (ϕ') is useful as an overall indicator of the growth rate when there is no constant trend in K and L_∞. Because ϕ' values obtained from this study (4.48 by FL and 4.55 by TL) were

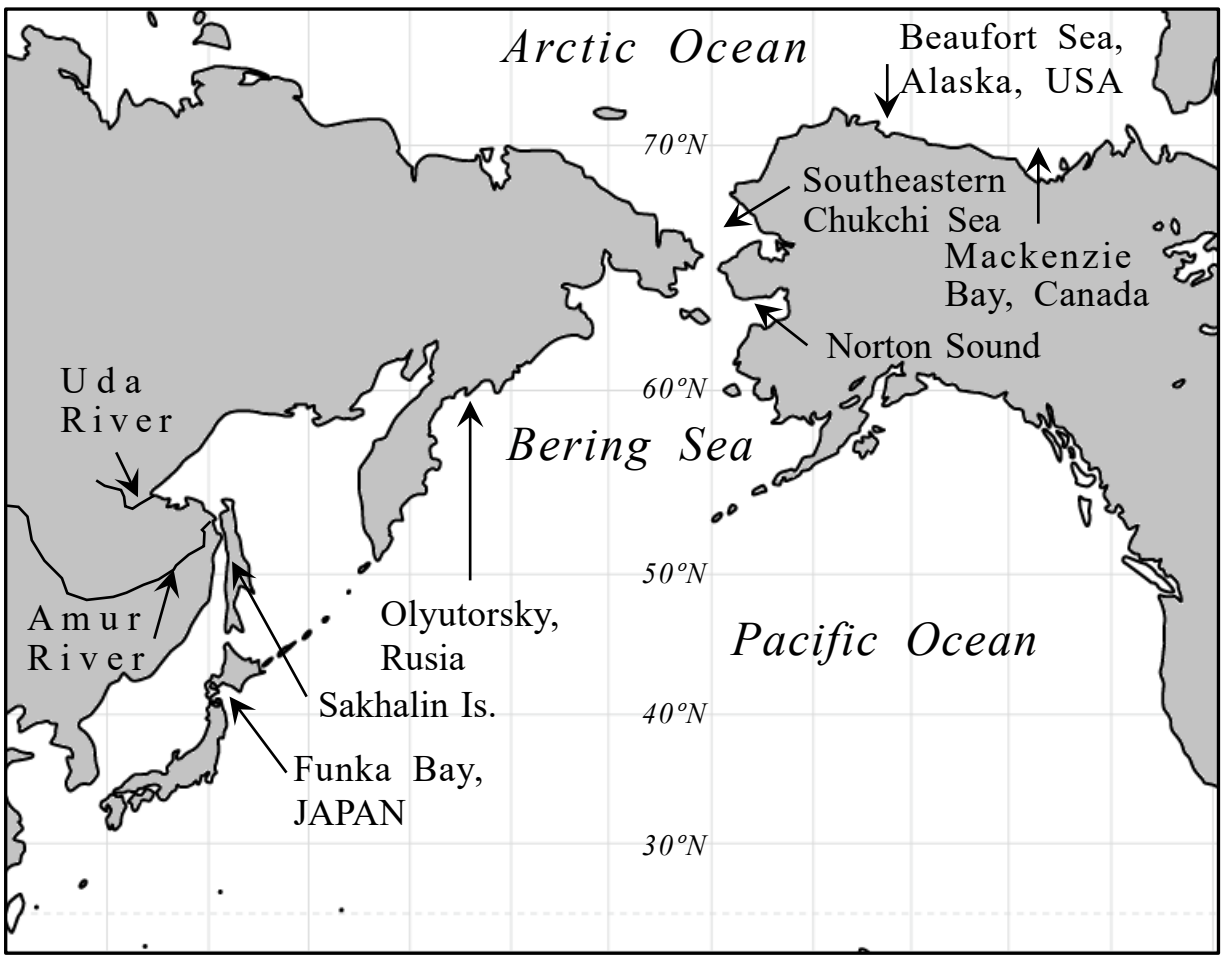


Fig. 3-11. Locations where growth patterns were compared in this study.

higher (indicating faster growth) than that of *O. dentex* collected in the Beaufort Sea (4.37 by FL) and Norton Sound (4.05 and 4.11 by TL; Table 3-3) and the maximum age in Funka Bay was less (6.8 years old) than other areas (8-10 years old), so the Funka Bay population inhabiting in a low latitude area grows faster during their younger age period agreeing with the trend hypothesized by Trip et al. (2014).

Another possibility for differences in growth performance among populations is differences in food availability between water environments. Osmeridae species feed on small fishes and invertebrates (Eschmeyer and Herald 1999) and fishes are important prey *for O. mordax dentex* as synonym of *O. dentex* (Haldorson and Craig 1984). In Funka Bay, *O. dentex* is one of the active-searching type predators in daytime and its primary foods are pelagic copepods for small-sized individuals and small fishes like Japanese anchovy *Engraulis japonicus* and juveniles of walleye pollock *Gadus chalcogrammus* for large-sized ones (see 4.3.2, Chapter 4), and zooplankton and walleye pollock juveniles are distributed abundantly (Yokoyama et al. 1989; Kendall and Nakatani 1992; Nakatani et al. 2007; Yamaoka et al. 2019). However, I do not have data at present to compare prey abundance between Funka Bay and the other habitats, so this explanation is a tentative one.

Many marine fishes are visual feeders, and light including light intensity and photoperiod can affect the ability to localize, catch, ingest the prey. Hence, light is an important factor to optimize the production of an active-searching type predator (Suthers and Sundby 1996; Boeuf and Le Bail 1999; Puvanendran and Brown 2002; Fielder et al. 2002; Aragon-Flores et al. 2017). Boeuf and Le Bail (1999) pointed out that day-length may indirectly modify growth of fish by increasing food intake or muscle mass by exercise. Suthers and Sundby (1996) showed that light conditions change with latitude and affect the growth and survival of fish. The mean annual day length at 70.3°N in the Beaufort Sea (13:07 ± 8:30: mean ± standard deviation), at 66.8°N in southeastern Chukchi Sea (13:10 ± 7:07), and at 64.6°N in Norton Sound (13:10 ± 5:55) are longer than

that at 42.3°N at river mouth of the Yamazaki River in Funka Bay (12:13 ± 2:07), and the seasonal variation is larger (National Astronomical Observatory of Japan 2021). Three habitats of *O. dentex* around Alaska are characterized by more extensive variations in photoperiod than Funka Bay, may not be optimal for growth of *O. dentex*, because *O. dentex* have limited time to find and feed on prey during the short daylength. Except for Funka Bay, all of the areas shown in Table 3-3 have periods when the sea surface is covered with ice or drift ice during winter and spring. Ice formation and drifts reduce daytime light intensity in the water and decrease the probability of finding prey.

Moreover, spawning migration of *O. dentex* varies from late April to early July and is likely linked to the latitude, for example, timing for spawning of *O. dentex* in Funka Bay and Amur River (ca. 42.3°N and 48.5°N, respectively) is from late April to mid-May, while that of Sakhalin and Uda River (ca. 51.0°N and ca. 54.8°N, respectively) begin from late May to mid-June (Belyanina 1968; Horikawa 1988; Inokuchi et al. 1997; Vasilets 2000; Ovsyannikov et al. 2019; Burlak and Zhukova 2020). Spawning periods of this species have not been clarified around Alaska, however it is assumed to be at least later than the spawning season in Funka Bay, when daylight hours are longer. Feeding of fish cease during the spawning period and the spawning period of *O. dentex* may coincide with the long daylength period in high latitude areas. This implies that the forage period of *O. dentex* population in high latitude areas may be shorter photoperiod or daylength than that of Funka Bay and this may contribute to slow growth of *O. dentex* of high latitude areas.

The minimum AIC values calculated from logistics, Gompertz, von Bertalanffy, and Richards models showed that the Gompertz equation was judged as the best fit model. According to Sakamoto et al. (1983), ΔAIC values greater than 1-2 can be acceptable as significantly different, but if it is smaller than 1 as insignificant. Logistic, Gompertz, and von Bertalanffy equations showed low ΔAIC with <1 in this study, and the goodness of fit from logistic,

Gompertz, and von Bertalanffy models was similar. ΔAIC of Richards model showed +2.0 to Gompertz model. Because the number of estimated parameters of the Richards model and the other three models are 4 and 3, respectively, the value 2.0 of ΔAIC showed only the difference in number of parameters. In addition, r^2 values of the four equations showed almost same values. Akamine (2010) described that Richards growth function also includes logistic, Gompertz, and von Bertalanffy growth function, *r* value in Richards growth function is the parameter which determines the shape of the growth curve, the growth curve converges to the Gompertz growth curve when *r* approaches 0. The *r* value of Richards function in this study showed 0.1 which is close to 0, implies that the Richards model shows close approximation to the Gompertz model for *O. dentex* in this study area. In conclusion, there was little difference in goodness of fit between these four growth equations. The reason for this was presumed to be that lower growth rates were not observed at a young age, since almost all data were larger than the inflection point showing the maximum growth rate.

Condition factor allows scientists to assess and compare the fatness between sexual maturity, age and sex differences and populations in different environments, and reflects seasonal changes in habitat (Kembenya et al. 2014; Keyombe et al. 2017); food supply (Le Cren 1951; Froese 2006); spawning season (Sekigawa et al. 2002; Santic et al. 2006; Zorica et al. 2006). Results in this study exposed that condition factor of *O. dentex* is close to 1 and reveal a slightly decreasing during the spawning period. Furthermore, the difference in condition factor between sexes were detected during spawning period, maximum GSI value of female was larger than that of male in spawning season (Fig. 3-9). This may be due to sex difference in the maturation energy required for the development of gonads even though the growth trajectories were similar. In other words, females of *O. dentex* in Funka Bay require more energy for gonadal enlargement than males, but given that there is no sex difference in

growth trajectory, it is possible that males spend more energy on spawning behavior such as run-up migration. Tag and recapture studies revealing that males of *O. mordax* are able to spawn multiples times (up to 4 times), while that of females rarely more than once during spawing season within a year (Murawski et al. 1980). However, at this point in time, I have not been able to obtain any specific data on the number of runs per spawning season for *O. dentex* in the Yamazaki River, which is supposed to be higher for males than for females.

In this chapter, I found that age determination of *O. dentex* by sagittal otolith was more accurate than by scale. In order to clarify why the growth rate of this species in Funka Bay and the Yamazaki River was higher than in other areas, the feeding habits and the abundance of available prey in the environment are discussed in the next chapter.

CHAPTER 4. FEEDING HABITS OF PACIFIC RAINBOW SMELT *O. DENTEX* AND SPECIAL REFERENCE TO FISH PREDATION IN FUNKA BAY, JAPAN

Abstracts

To clarify the nutritional substrates of food, the annual life cycle, and growth performance of Pacific rainbow smelt (*Osmerus dentex*), I caught and investigated the stomach content of 316 specimens in Funka Bay from October in 2018 to December in 2019 and in the Yamazaki River from late April in 2019 to mid May in 2019. Nineteen prey species were identified from stomach contents of *O. dentex*. Pisces (fishes such as Japanese anchovy *Engraulis japonicus,* and juveniles of walleye pollock *Gadus chalcogrammus,* and other three demersal fish juveniles) occupied the highest *%IRI* (80.2%) as the main prey items of *O. dentex*, following that, Decapoda Natantia (shrimps such as *Crangon dalli* and *Neocrangon* sp.; *%IRI*=6.2), pelagic Copepoda (*Calanus pacificus*; *%IRI*=5.6), Mysidacea (mainly *Neomysis japonica*; *%IRI*=4.7), and Amphipoda Gammaridea (seven demersal species; *%IRI*=3.1) constituted relatively high proportions. Ontogenetic diet shift of *O. dentex* was observed and, *O. dentex* with < 150 mm SL fed on crustaceans (natant decapods, pelagic *C. pacificus*, mysidaceans, and gammarids), while that with size > 151 mm SL fed mainly on fishes (the range of *%IRI*: 55.2-86.9%). High percentage of empty stomach (*%VI*=73) was observed in *O. dentex* and that in the Yamazaki River (*%VI*=88) was higher than that in Funka Bay during spawning period (April-May). Low %IRI of prey fishes during April-May may be caused by low prey require in spawning period for *O. dentex* and low encounter rates caused by spatial mismatch to walleye pollock juveniles for low abundances and that with inadequate low water temperature for Japanese anchovy.

4.1. Introduction

Stomach content analysis of fish is a popular method to study the trophic ecology of teleost and provides the information of the diet (Hyslop, 1980), it is essential for elucidating the life cycle and stock fluctuation mechanisms of fishes. For example, bias in the food composition of a fish species is an important factor in defining the spatial distribution of that species. Differences in the quality (mainly digestibility and energy content) and quantity of the prey available to them can have a profound effect on their subsequent growth rate and nutritional status, as well as on the timing of maturation and the number of eggs conceived.

Information on the feeding ecology of animals is critical for understanding trophic interrelations of population and community dynamics within an ecosystem and for comparisons among systems (Amundsen and Sánchez-Hernández 2019). Bachok et al. (2004) stated that information on the feeding habit of marine fish is beneficial to assess the role of marine fish in the ecosystem. Moreover, the study of the feeding habits of marine fish is necessary for fish stock assessment and ecosystem modeling as some major models and methods like methods of multi-species virtual population analysis (Sparre 1991; Bulgakova et al., 2001).

Previous studies on the feeding habits of Pacific rainbow smelt *O. dentex* are limited and were carried out in the outer Mackenzie delta (Percy 1975) and Alaskan Beaufort Sea (Haldorson and Craig 1984), in which the authors reported that the important diet of *O. dentex* consisted of fish, mysids, and amphipods. *O. dentex* plays an important role in functioning of biological community in coastal waters. The species not only acts as a food source for predatory fishes but also competes for food with other fish species (Datsky 2016; 2017). However, the feeding habits of Funka Bay population, which has a high growth rate among the populations of this species (see Chapter 3), are not yet known. The aims of this study are to clarify the diet of *O. dentex* in Funka

Bay, and to elucidate the factors that achieve high growth rate from the feeding ecology.

4.2. Materials and Methods

Samples of demersal fishes inclusive of *O. dentex* were conducted with two types of otter trawl nets with the same mouth width along the sea bottom from T/S *Ushio-maru* of Hokkaido University, Faculty of Fisheries at 10 sampling stations (Fig. 3-1) in Funka Bay from December in 2015 to May in 2021 excluded in July. An otter trawl net with sleeves (the distance between the tips of the sleeves: 10.4 m, net mouth height: 1.5 m, and mesh size in the cod-end: 12 mm; Yokoyama et al., 1989) was used in August each year and in October when there were not enough towing times in August and another otter trawl net without sleeves (net mouth width: 10.4 m, net mouth height: 2.5 m, and mesh size in the cod-end: 12 mm; Maeda et al., 1979) was used in other months. In addition, samples of *O. dentex* were collected at the mouth of the Yamazaki River with a scoop net from late April to mid May in 2019. Fish samples were immediately frozen or refrigerated after capture and brought back to the laboratory for further examination. Specimens of *O. dentex* collected from October in 2018 to December in 2019 were used for dietary analysis.

In laboratory, individuals of *O. dentex* were thawed, the standard length (SL) and total length (TL) were measured to the nearest 1 mm. Stomachs were removed and stored in 4% buffered formaldehyde solution (i.e., 10% buffered formalin solution). The stomach contents were identified to the lowest practical taxa under a binocular microscope and counted and weighed to the nearest 0.001 g by wet weight.

Data on stomach contents were expressed as the following indices. The stomach fullness index (*%FI*) which was expressed as weight percent of stomach contents to the body weight of fish was analyzed. The vacuity index (*%VI*) which was expressed as percent occurrence frequency of the empty stomachs to total number of stomachs was analyzed.

The importance of food items in the diet was determined as the percentage index of relative importance ($\%IRI_i$; Pinkas et al. 1971; Hyslop 1980):

$$IRI_i = (\%N_i + \%W_i) \times \%F_i$$

$$\%IRI_i = IRI_i \times 100/\sum IRI$$

where percentage frequency of occurrence ($\%F_i$: the percentage of *O. dentex* that consumed prey type *i*), percentage composition by number and percentage composition by weight ($\%N_i$ and $\%W_i$ being, respectively, the percentage of each prey type *i* of the total number and weight of prey type *i*).

Abundances of prey fishes at each sampling stations (density: number of individuals per 10,000 m^2 and biomass: wet weight in kg per 10,000 m^2) were calculated from net mouth widths (both 10.4 m) and the towing distance on the bottom integrated by the electromagnetic log. It was assumed that the filtration efficiency of each trawl net was 100%.

%FI and *%IRI* were compared between sexes using *t*-test and between body size classes using one-way ANOVA and Scheffé's multiple comparison. *%VI* was compared between sampling months using χ^2-test. Significant level was set at 5%. Statistical analyses were performed using SPSS 20.

4.3. Results

4.3.1. Frequency of empty stomach individuals and feeding intensity

A total of 316 specimens of Pacific rainbow smelt *O. dentex* examined for dietary analysis and 160, 129, and 27 individuals were males, females, and immatures, respectively. Body size ranges were 94-269 mm SL and 6.96-212.3 g in body weight (Fig. 4-1). Of total 316 stomachs examined, 85 stomachs contained food items and 231 were empty *(%VI*=73%). Vacuity index (*%VI*) showed low in March (43%) and August (38%) and high in April, May, September and October (56-85%; Fig. 4-2 upper). *%VI* showed small variation among size classes (65-80%; *P*=0.93, χ^2-test; Fig. 4-2 lower). The stomach fullness index (*FI*) varied from 0.002% to 9.78% by individual and mean *FI* was

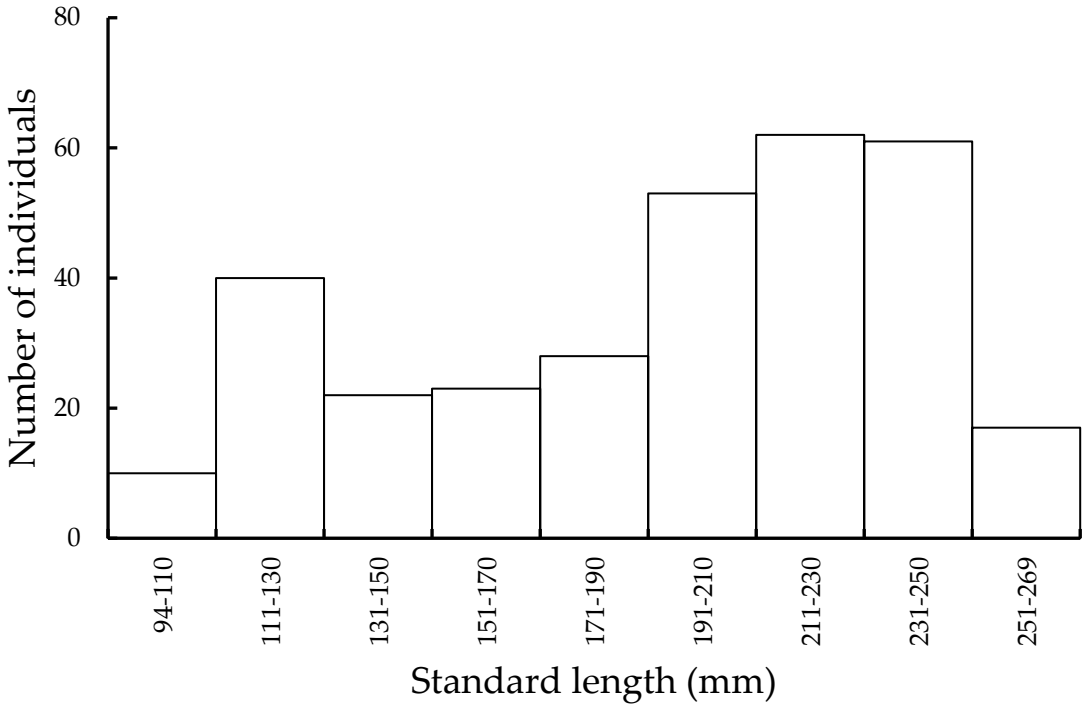


Fig. 4-1. Body size distribution of Pacific rainbow smelt *Osmerus dentex* for dietary analysis in this study.

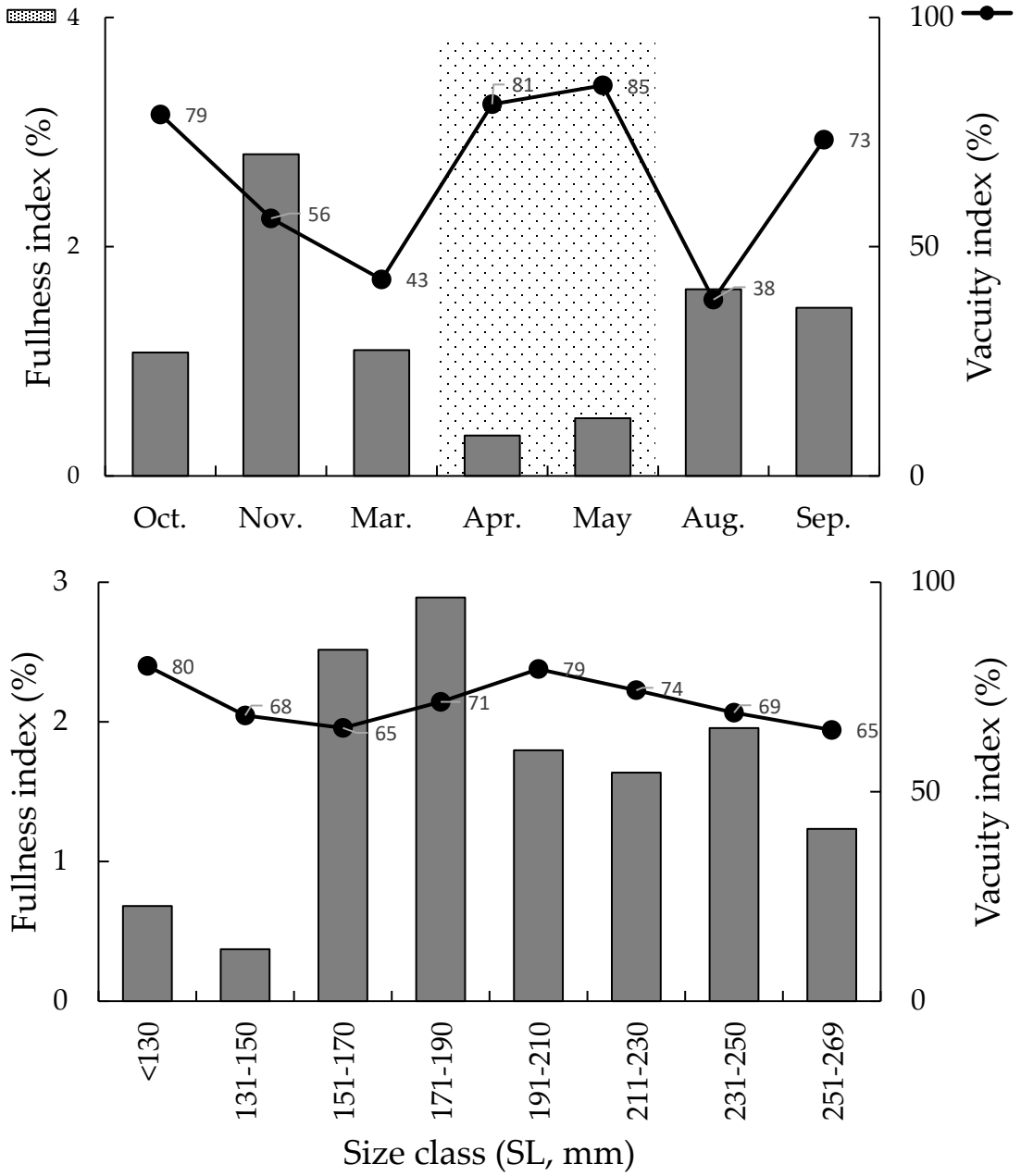


Fig. 4-2. The mean fullness index (*FI*) and vacuity index (*%VI*) of stomachs for month (A) and size class (B) in Pacific rainbow smelt *O. dentex* in Funka Bay and the Yamazaki River. Dotted area shows spawning period.

1.67%. There were no significant differences in mean *FI* values between male and female (P=0.23; t-test) and among size classes (P=0.26; one-way ANOVA) Mean *FI* in April and May were significantly lower than that in November (P=0.049 and P=0.004, respectively; Scheffé's multiple comparison).

Mean *%VI* and *FI* were compared between samples of *O. dentex* collected in Funka Bay and the mouth part of the Yamazaki River during spawning period (April and May; Fig. 4-3). *%VI* in the Yamazaki River (88%) was significantly higher than that in Funka Bay (50%; P=0.002; χ^2-*test*). *FI* in the Yamazaki River (0.47%) was significantly lower than that of Funka Bay (1.95%; P=0.001, t-test).

4.3.2 Composition of food items

Food items in stomachs were identified to 19 taxonomic groups (Table 4-1-1). The dominant *%IRI* (> 50%) of *O. dentex* was fishes (Pisces: 80.2%), followed by shrimp (Decapoda Natantia: 6.2%), a species of pelagic copepoda (*Calanus pacificus*: 5.6%), mysids (Mysidacea: 4.7%), and gammarid amphipods (Amphipoda Gammaridea: 3.1%). Five taxonomic species of fishes were identified in the stomach content, and those were inclusive of Japanese anchovy *Engraulis japonicus* (*%IRI*=47.6), walleye pollock *Gadus chalcogrammus* juveniles (16.4%), Pacific cod *G. macrocephalus* juveniles (*%IRI*=3.0), snail-fin poacher *Podothecus sachi* (1.3%), and stone flounder *Platichthys bicoloratus* (< 0.1%). *Calanus pacificus (%IRI*=5.6) was the only copepod to appear in the stomach of *O. dentex*. *Crangon dalli* (*%IRI*=2.8) and *Neocrangon* sp. (2.1%) occupied major parts of shrimp (Decapoda Natantia) in stomachs of *O. dentex*. *Neomysis japonica* (*%IRI*=2.7) showed dominant in identifiable mysids. Cumaceans (*%IRI*=0.2), isopods (<0.1%), and invertebrates' eggs (< 0.1%) showed low proportions in the diet.

Composition of food items in the stomach content of *O. dentex* caught in Funka Bay was listed in Table 4-1-2. Fishes occupied dominant percentage (*%IRI*=83.9) with the predominant of Japanese anchovy *E. japonicus* (52.3%),

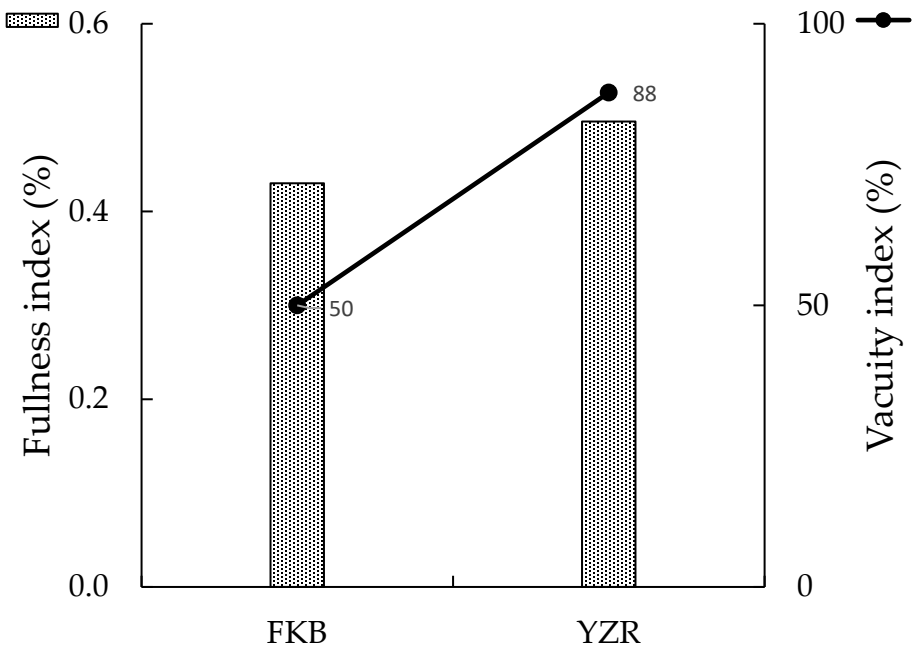


Fig. 4-3. The mean fullness index (*FI*) and vacuity index (*%VI*) in Pacific rainbow smelt *O. dentex* in Funka Bay and the Yamazaki River during spawning season.

Table 4-1-1. Percentage frequency of occurrence (*%F*), percentage composition by number (*%N*), percentage composition by weight (*%W*), index of relative importance (*IRI*), and *%IRI* of prey items found in stomachs of Pacific rainbow smelt *O. dentex* (*n*=316) in Funka Bay and the Yamazaki River

Taxa	Number of prey items in stomach	Number of stomachs with prey	Prey weight (g)	*%F*	*%N*	*%W*	*IRI*	*%IRI*
Pisces (total)	77	51	107.5	60	15.5	93.1	1606.3	80.2
Engraulis japonicus	19	16	54.1	19	3.8	46.8	953.1	47.6
Gadus chalcogrammus	12	11	26.6	13	2.4	23.0	328.8	16.4
Gadus macrocephalus	6	4	13.4	5	1.2	11.6	60.4	3.0
Podothecus sachi	21	4	1.4	5	4.2	1.2	25.6	1.3
Platichthys bicoloratus	3	1	0.2	1	0.6	0.2	0.9	<0.1
Unidentified Pisces	16	15	11.8	18	3.2	10.2	237.5	11.9
CRUSTACEA								
Decapoda Natantia (total)	49	23	4.4	27	9.8	3.8	123.1	6.2
Crangon dalli	18	9	1.9	11	3.6	1.6	55.4	2.8
Neocrangon sp.	14	9	1.2	11	2.8	1.1	41.2	2.1
Unidentified Natantia	17	5	1.3	6	3.4	1.1	26.6	1.3
Mysidacea (total)	70	15	2.2	18	14.1	1.9	93.8	4.7
Neomysis japonica	23	8	1.4	9	4.6	1.2	55.0	2.7
N. mirabilis	8	1	0.4	1	1.6	0.4	2.3	0.1
Gasstrosaccus vulgaris	1	1	0.1	1	0.2	0.1	0.3	<0.1
Acanthomysis longirostris	1	1	<0.1	1	0.2	<0.1	0.3	<0.1
Unidentified Mysidacea	37	4	0.2	5	7.4	0.2	35.9	1.8
Amphipoda Gammaridea (total)	56	16	1.0	19	11.2	0.9	62.2	3.1
Amanogammarus annandalei	8	2	0.1	2	1.6	0.1	3.9	0.2
Monoculodes japonicus	12	1	0.1	1	2.4	0.1	2.9	0.1
Byblis japonicus	2	2	0.1	2	0.4	0.1	1.1	0.1
Melita sp.	2	1	<0.1	1	0.4	<0.1	0.5	<0.1
Monoculodes carinatus	1	1	<0.1	1	0.2	<0.1	0.2	<0.1
Pseudorchestoidea brito	1	1	<0.1	1	0.2	<0.1	0.2	<0.1
Gammarus nipponensis	1	1	<0.1	1	0.2	<0.1	0.2	<0.1
Unidentified Gammaridea	29	7	0.7	8	5.8	0.6	53.0	2.6
Copepoda (*Calanus pacificus*)	237	2	0.2	2	47.6	0.2	112.4	5.6
Cumacea	7	2	<0.1	2	1.4	<0.1	3.4	0.2
Isopoda	1	1	<0.1	1	0.2	<0.1	0.3	<0.1
INVERTABRATES (egg)	1	1	0.2	1	0.2	0.2	0.5	<0.1
Total	498	111	115.5					
Number of stomachs examined	316							
Number of stomachs with prey	85							
Number of empty stomachs	231							

Table 4-1-2. (cont. in Funka Bay)

Taxa	Number of preys in stomach	Number of stomachs with its prey	Prey weight (g)	*%F*	*%N*	*%W*	*IRI*	*%IRI*
Pisces (total)	51	44	104.6	64	12.9	97.1	2048.4	83.9
Engraulis japonicus	19	16	54.1	23	4.8	50.2	1275.3	52.3
Gadus chalcogrammus	12	11	26.6	16	3.0	24.7	441.5	18.1
Gadus macrocephalus	6	4	13.4	6	1.5	12.5	81.0	3.3
Unidentified Pisces	14	13	10.5	19	3.5	9.8	250.6	10.3
Crustacea								
Natantia (total)	39	17	2.1	25	9.9	2.0	112.6	4.6
Crangon dalli	18	9	1.9	13	4.6	1.7	82.0	3.4
Neocrangon sp.	8	5	0.2	7	2.0	0.2	16.0	0.7
Unidentified Natantia	13	3	0.1	4	3.3	0.1	14.6	0.6
Mysidacea (total)	32	5	0.2	7	8.1	0.2	34.8	1.4
Neomysis japonica	3	2	0.2	3	0.8	0.2	2.7	0.1
Unidentified Mysidacea	29	3	0.1	4	7.3	0.1	32.1	1.3
Amphipoda Gammaridea (total)	29	8	0.6	12	7.3	0.6	64.8	2.7
Byblis japonicus	1	1	<0.1	1	0.3	<0.1	0.4	<0.1
Unidentified Amphipoda	27	6	0.6	9	6.8	0.5	64.1	2.6
Copepoda (*Calanus pacificus*)	237	2	0.2	3	60.0	0.2	174.4	7.1
Cumacea	7	2	<0.1	3	1.8	<0.1	5.2	0.2
Total	395	78	107.8					
Number of stomachs examined	185							
Number of stomachs with prey	69							
Number of empty stomachs	116							

Table 4-1-3. (cont. in the Yamazaki River)

Taxa	Number of preys in stomach	Number of stomachs with its prey	Prey weight (g)	*%F*	*%N*	*%W*	*IRI*	*%IRI*
Pisces (total)	26	7	2.9	44	25.2	37.6	1236.0	33.0
Podothecus sachi	21	4	1.4	25	20.4	18.3	966.9	25.9
Platichthys bicoloratus	3	1	0.2	6	2.9	2.3	32.5	0.9
Unidentified Pisces	2	2	1.3	13	1.9	17.0	236.6	6.3
Crustacea								
Decapoda Natantia (total)	10	6	2.3	38	9.7	29.1	726.5	19.4
Neocrangon sp.	6	4	1.0	25	5.8	13.5	483.5	12.9
Unidentified Natantia	4	2	1.2	13	3.9	15.5	242.9	6.5
Mysidacea (total)	38	10	1.9	63	36.9	25.0	1494.4	40.0
Neomysis japonica	20	6	1.2	38	19.4	16.0	1329.3	35.5
N. mirabilis	8	1	0.4	6	7.8	5.3	81.9	2.2
Gasstrosaccus vulgaris	1	1	0.1	6	1.0	1.0	12.0	0.3
Acanthomysis longirostris	1	1	<0.1	6	1.0	0.3	8.2	0.2
Unidentified Mysidacea	8	1	0.2	6	7.8	2.3	63.0	1.7
Amphipoda Gammaridea (total)	27	8	0.4	50	26.2	5.2	250.9	6.7
Amanogammarus annandalei	8	2	0.1	13	7.8	1.0	109.2	2.9
Monoculodes japonicus	12	1	0.1	6	11.7	1.3	81.2	2.2
Byblis japonicus	1	1	0.1	6	1.0	0.8	10.8	0.3
Melita sp.	2	1	<0.1	6	1.9	0.1	12.8	0.3
Monoculodes carinatus	1	1	<0.1	6	1.0	0.1	6.6	0.2
Pseudorchestoidea brito	1	1	<0.1	6	1.0	0.1	7.0	0.2
Unidentified Amphipoda	2	1	0.1	6	1.9	1.8	23.4	0.6
Isopoda	1	1	<0.1	6	1.0	0.2	7.5	0.2
Invertabrata (egg)	1	1	0.2	6	1.0	3.0	24.7	0.7
Total	103	33	7.8					
Number of stomachs examined	131							
Number of stomachs with prey	16							
Number of empty stomachs	115							

followed by a pelagic copepod of *C. pacificus* (7.1%), shrimps (4.6%). Gammarids (*%IRI*=2.7) and mysids (1.4%) were less dominant in the diet.

Mysids were the most common prey in the stomach contents of *O. dentex* in the mouth part of the Yamazaki River (*%IRI*=40.0; Table 4-1-3). Following by fishes (*%IRI*=33.0), shrimps (19.4%), and gammarids (6.7%). *N. japonica* (35.5%) showed the dominant part in identifiable mysids. Stone flounder *P. bicoloratus* (*%IRI*=25.9) was the main component in identifiable fishes. Japanese anchovy *E. japonicus* and walleye pollock *G. chalcogrammus* were not detected in the stomach of *O. dentex* collected in the Yamazaki River.

4.3.3. Seasonal changes in stomach contents

From August to November, fishes occupied 56.5-86.8% in *%IRI* in the stomachs of *O. dentex* (Fig. 4-4). In September, cumaceans showed relatively higher *%IRI* (33.7%) than other months. In March, gammarids showed major part in the stomach contents of *O. dentex (%IRI*=85.7). In April and May, there was not prey items with > 50% in *%IRI*, and four prey items as fishes (20.2-36.5%), shrimps (23.8-33.0%), gammarids (7.4-35.4%), and mysids (10.0-31.4%) were relatively common than others.

4.3.4. Ontogenetic shift of stomach contents

Eighty percent of *O. dentex* with < 130 mm SL (40 of 50 individuals) had empty stomachs, and the remaining 20% were feeding on shrimps (*IRI%*=53.8), gammarids (24.2%), and pelagic copepod of *C. pacificus* (22.0%; Fig. 4-5). In size class of 131-150 mm SL, *C. pacificus* showed 39.3% in *%IRI*, followed by mysids (29.0%) and gammarids (21.7%). *O. dentex* with > 151 mm SL mainly fed on fishes (*%IRI* ranged in 55.2-86.9%). Smallest *O. dentex* which had consumed fishes was 156 mm SL (184 mm TL). Crangonid shrimps (*Crangon dalli* and *Neocrangon* sp.) showed relatively high *%IRIs* in 151-170 mm SL and 171-190 mm SL (42.7% and 27.2%, respectively). Mysids occupied relatively high *%IRIs* in 211-230 mm SL and 251-289 mm SL (15.4% and 14.8%,

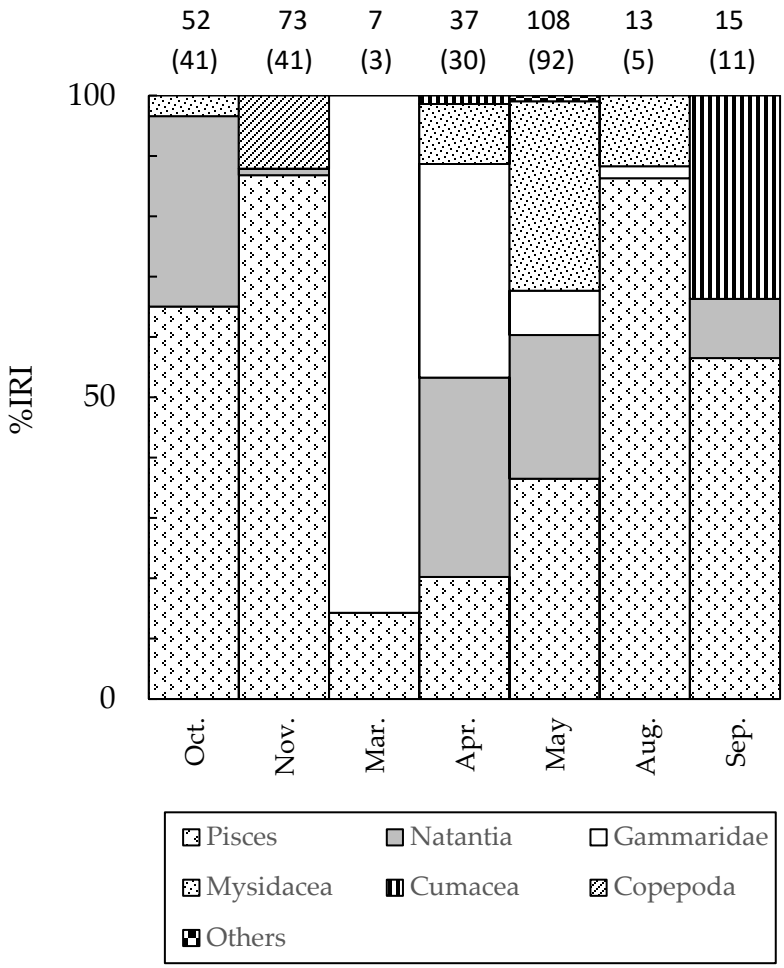


Fig. 4-4. Monthly changes in the percentage index of relative important (*%IRI*). Number of fish examined and number of fish with empty stomachs in the parentheses were shown above each bar.

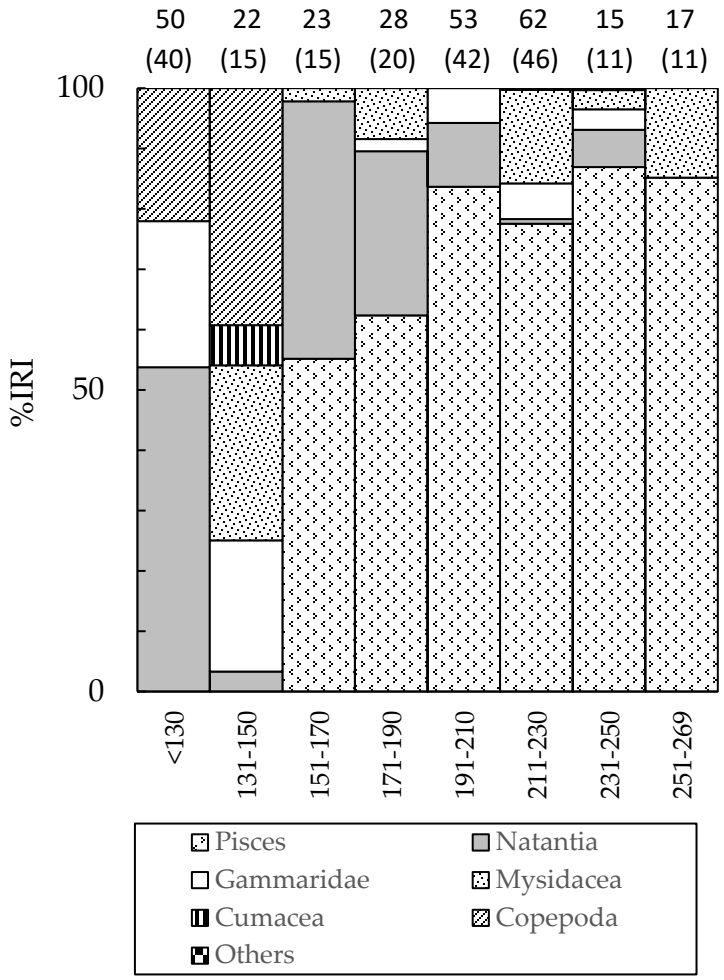


Fig. 4-5. Ontogenetic shift in the percentage index of relative important (*%IRI*). Number of fish examined and number of fish with empty stomachs in the parentheses were shown above each bar.

respectively).

4.3.5. Abundances of prey fishes in environment

Walleye pollock *G. chalcogrammus* juveniles were collected by two types of otter trawl nets on the sea-bottom of 57-98 m depth stations in Funka Bay through the year (Fig. 4-6). Higher abundances of the juveniles were recorded from June to November than those from December to May exclusive of the mean value during May 14-16 in 2019 (4,850 ± 3,133 inds./10,000 m^2 and 3.04 ± 1.59 kg/10,000 m^2; mean ± standard deviation).

Japanese anchovy *E. japonicus* was collected from 57-98 m water depth stations from late August to mid-December, but not from January to June (Fig. 4-6). The highest mean abundances were recorded during October 28-29 in 2019 (923.7 ± 906.6 inds./10,000 m^2) and October 4-5 in 2018 (8.23 ± 8.16 kg/10,000 m^2).

4.4. Discussion

Prey similarities were observed among the different geographic populations, and dominant prey items of *O. dentex* were fishes (Pisces) and crustaceans (Mysidacea, Copepoda, Amphipoda Gammaridea, and Decapoda Natantia; Table 4-2). Although, results from this study and previous studies showed that there is slightly variation Percy (1975) reported that the diet of *O. dentex* included Amphipoda, Isopoda, Mysidacea, Coleoptera, and Pisces in the outer Mackenzie delta. *O. dentex* caught in Mackenzie Bay in Beaufort Sea fed on Amphipoda, Cumacea, Isopoda, Mysidacea, Insecta, and Plantae (Poulin 1976). Haldorson and Craig (1984) reported the appearance of Mysidacea, Amphipoda, Isopoda, Pisces, and Polychaeta in the stomach of *O. dentex* in the coastal waters of Beaufort Sea, Alaska, USA. While *O. dentex* in the Korf-Karagin coastal area of the Southwestern Bering Sea consumed Polychaeta, Mysidacea, Amphipoda, Euphausiacea, Natantia, Insecta and Pisces (Karpenko and Vasilets 1996). This variation in the diet composition may be caused by the different in

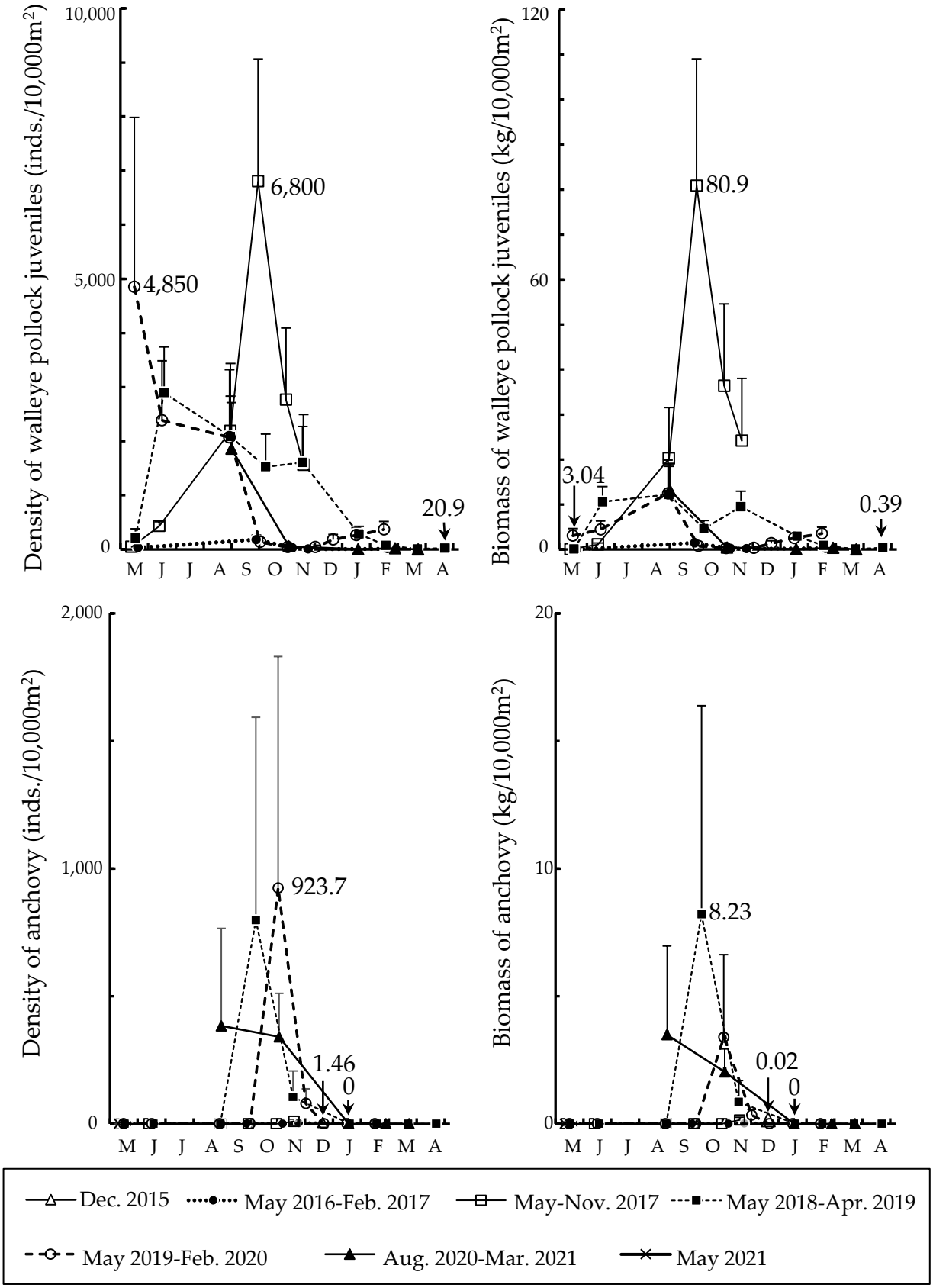


Fig. 4-6. Mean density and biomass of walleye pollock *Gadus chalcogrammus* juveniles and Japanese anchovy *Engraulis japonicus* collected with two types of otter trawl nets towing along the sea-bottom (57–es98 m depth) in Funka Bay from December 2015 to May 2021. Error bars show standard deviations. Characters without error bars indicate data obtained from a single towing.

Table 4-2. Comparison of food items in *O. dentex* from different habitats

Area	Littoral zone in Kort – Karagin, RUS	Offshore waters in the Kort – Karagin, RUS	Outer of Mackenzie Delta, CA	East Mackenzie bay, CA	Beaufort Sea, AK, USA	Funka Bay, JP
	Polychaeta	Polychaeta	Amphipoda	Amphipoda	Mysidacea	Pisces
	Mysidacea	Mysidacea	Isopoda	Cumacea	Amphipoda	Natantia
	Amphipoda	Cumacea	Mysidacea	Isopoda	Isopoda	Amphipoda
	Euphausiacea	Natantia	Coleoptera	Mysidacea	Pisces	Mysidacea
	Insecta	Reptantia (larva)	Pisces	Crustaceana	Polychaeta	Copepoda
	Pisces	Decapodiforms	Chironomidae	Pisces		Cumacea
	Natantia	Pisces	Copepoda	Plantae		Isopoda
				Debris		Eggs
Source	Karpenko and Vasilets (1996)	Karpenko and Vasilets (1996)	Percy (1975)	Poulin (1976)	Haldorson and Craig (1984)	This study

environmental factors; and in distribution, density, abundance, and availability of prey items (Rask 1983; Dorner et al. 2003; Santic et al. 2003; Taal et al. 2014; Yazicioglu et al. 2016). The reason for the presence of predation on pelagic copepod *C. pacificus* but the absence of polychaetes predation in Funka Bay is examined in terms of prey abundance. The high zooplankton and benthos abundances in Funka Bay are supported by high primary production and phytoplankton biomass compared to other surrounding waters (Kido and Ohtani 1981), so it is unlikely that food shortage is the cause of diet shift, and in fact the growth rate of *O. dentex* in Funka Bay is higher than in other waters. The morphology of mouth of *O. dentex* is the largest in the family Osmeridae, and the lower jaw protrudes more than the upper jaw, making it more suitable for feeding on plankton than on benthos. It also has two large, sharp teeth on its upper jaw and many fine teeth on its lip, allowing it to feed on large fish. When the encounter rate to prey fishes is low, *O. dentex* would be able to switch their diet to zooplankton.

O. dentex be divided into 2 group based on the feeding habits: (i) small sized group (<150 mm SL) which characterized by the missing of fishes (Pisces) in diet and the important of shrimps (Decapoda Natantia), mysids (Mysidacea), and gammarids (Amphipoda Gammaridea) in the stomach content; (ii) large sized group (>150 mm SL) which characterized by the predominant of fishes in the diet. This implies that there was a noticeable ontogenetic shift in the feeding habits of *O. dentex*. This shift in food were documented by many authors. Yazicioglu et al. (2016) noticed a shift from macroinvertebrates to fish in the diet of European perch *Perca fluavitilis* when perch reached a total length above 182 mm. Horinouchi et al. (1996) reported ontogenetic shift in puffer fish *Takifugu pardalis*. Belyanina (1969) reported that the assortment of food component, size and quantity change with growth of rainbow smelt *O. eperlanus*; the important of Pisces prey increase with age, and hence the size. Vinni et al. (2004) recorded that the probability of zooplankton ingestion decreased and that of fish increased with total length of European rainbow smelt *O. eperlanus*. Dermott et

al. (1999) found that fish prey in *O. mordax* was strongly correlated with *O. mordax* size; Pisces prey has only consumed by *O. mordax* with > 170 mm FL. A marked increase in piscivorous feeding for *O. mordax* longer than 180 mm TL had also been reported by Foltz and Norden (1977a). Doherty and McCarthy (2004) presented a mean length of 190.6 mm TL for piscivorous European rainbow smelt *O. eperlanus*. Karpenko and Vasilets (1996) described that smaller *O. mordax dentex* (< 169 mm TL) ate mostly mysids, amphipods, and polychaetes; while larger *O. mordax dentex* with mean size of 208 mm TL fed mainly on young fishes. In this study, I found that the smallest *O. dentex* which had consumed fishes was 156 mm SL (184 mm TL), and this size is similar to the biological minimum size of *O. dentex* which were 148 mm SL on female (Inokuchi et al. 1997). Thus, the increased prey requirements of *O. dentex* may be one of the factors driving the shift to diets with higher energy content.

Results from this study also revealed the differences in the diet composition between the Funka Bay and the Yamazaki River of *O. dentex* (Tables 4-1-2; 4-1-3). The highlighted difference was the dominance of fish prey in Funka Bay (*%IRI* = 73.5), while that of the Yamazaki River was mysids (*%IRI* = 40) and piscivory only contributed 30% of *%IRI*. Similar result has been reported by Karpenko and Vasilets (1996) that piscivory was dominated for *O. dentex* in the open water of Karagin Bay (with 62-100% smelt fed on fishes), but the diet in littoral zone were crustacea and polychaetes, and fishes occupied only 3.3-38% in *F%*.

The seasonal changes in the diet of Osmeridae have been reported in previous studies (Belyania 1969; Burbidge 1969; Foltz and Norden 1977b; Karpenko and Vasilets 1996; Doherty and McCarthy 2004; Vinni et al. 2004; Rooney and Paterson 2009; Taal et al. 2014), and those of *O. dentex* have been reported (Faltas 1996; Dadebo et al. 2014). In Funka Bay for *O. dentex*, Pisces, which making up to 80.2% in *%IRI*, were the most dominant food items and might be important prey item. Among the Pisces, Japanese anchovy *E. japonicus*

was the most important (*%IRI*=31.4); followed by walleye pollock *G. chalcogrammus* juveniles (9.5%). Our results also showed the seasonal changes in the diet composition of *O. dentex* (Fig. 4-4). Shrimps were eaten by *O. dentex* throughout the year. Fishes were also consumed throughout the year but with the obviously predominance from August to November. Gammarids occupied large part of N%s from March to May and mysids showed occupied the major part from April to August in *N%*. Walleye pollock juveniles (young of the year: 0+) are distributed along the bottom in <15℃ water through the year in the bay (Nakatani and Maeda 1987), and I have confirmed the perennial occurrence of walleye pollock juveniles. In addition, I have shown that the juveniles show high abundance from June to November in Funka Bay. In this area, pollock juveniles settle from late May to July and abundance declines as the month progresses because some juveniles remain in the bay but others migrate out of the bay and some die (Nakatani and Maeda 1987). In contrast, Japanese anchovy is distributed in 11-31°C (Hayasi 1967) and it is abundant in 15-30°C (Tsuruta 2006), this prey item is distributed from June to December in Funka Bay (Kinoshita 1962). While temperature of Funka Bay is lower than these temperature ranges from March to May due to the influence of cold Coastal Oyashio Water (Kido and Ohtani 1981). Japanese anchovy, collected by the same haul as *O. dentex* shown in this study, also appeared from August to December, except in July when no survey was carried out. Therefore, it is assumed that *O. dentex* can obtain high growth rates by feeding on pollock juveniles from May after spawning to August, and by switching to anchovy from late August to December when pollock abundance declines. It is thought that *O. dentex* flexibly change their prey regardless of whether they are demersal fishes or nekton as the fish fauna changes with changes in the water temperature environment. Low percentage of piscivory during March and May in this study may occur low encountering rate to walleye pollock juveniles and Japanese

anchovy. The temporal variation in feeding activity among populations during the foraging period of *O. dentex*, although not specific, could be explained by the scarcity of food items during some periods (Timola 1980; Taal et al. 2014).

The GSI values of males were relatively high from November to February and those of females from January to February (although the data were obtained from only two females: Fig. 3-9) in Funka Bay. The period from November to April may be regarded as "gonadal development period" rather than "feeding period", and sufficient food is available by November, less vigorous feeding may be necessary. Winter samples of *O. dentex* are inadequate and need to be supplemented with these data to further clarify the annual life cycle in the future.

The overall *%VI* value of Pacific rainbow smelt *O. dentex* was remarkably high at 73%, and stomach of 88% of the spawn runners were empty in the Yamazaki River, but non-runners were lower (50%) in Funka Bay (Fig. 4.3). This would be explained by the spawning behavior of *O. dentex*: the lowest feeding activity period is in concordance with the spawning period of *O. dentex* in Funka Bay which is usually start from late April and finish in mid-May (Horikawa 1988). High incidence of empty stomach of *O. dentex* has been reported in previous studies, particularly around the spawning time (Percy 1975; Poulin 1976; Haldorson and Craig 1984). Percy (1975) reported that adult *O. dentex* showed high empty stomachs rate (*%VI*=89%) in Mackenzie delta, Canada and the Korf-Karagin coastal area of the Southwestern Bering Sea, Russia (Karpenko and Vasilets 1996). A similar finding has also been reported by Vasilets (2000) on *O. dentex* from Kamchatka. Haldorson and Craig (1984) reported that the range of *%VI* in *O. mordax dentex* (synonym of *O. dentex*) was 97-100% in the coastal water of Beaufort Sea, Canada during spawning season from March to May. According to Sakamoto (1982), feeding activity of fish changes with the variation of seasonal water temperature and food items, abundance of fish and spawning time. Although some fishes have the highest

percentage of *FI* during spawning season to meet the reproduction requirement (Froese and Pauly 2000; Farrag 2014; Osman et al. 2013), it seems that unlike these fish species, *O. mordax dentex* were reported to cease feeding while undergoing spawning migration in the outer Mackenzie delta, Canada (Percy 1975); the Korf-Karagin coastal area of the Southwestern Bering Sea (Karpenko and Vasilets 1996); and Kamchatka, Russia (Vasilets 2000).

This chapter presents the primary qualitative and quantitative data describing the diet of Pacific rainbow smelt *O. dentex* in Funka Bay and the mouth part of Yamazaki River, Hokkaido, Japan. The result in this study suggests that *O. dentex* is one of piscivory predators and top-down members of ecosystem in the demersal fish assemblage. These results contribute the fundamental information that helps to improve our knowledges about ecology and biology of this species.

CHAPTER 5. EFFECTS OF ENVIRONMENT ON THE EMBRYO AND LARVAL DEVELOPMENT OF *O. DENTEX*

Abstracts

This study was conducted to determine the effects of different temperatures (8, 10, 12 and 14°C) and salinities (0, 8, 16, 24 and 32psu) on hatching success and embryonic period, as well as the effects of salinities (0, 8, 16 and 24psu) on the development of early larval stage of *O. dentex*. Results showed that embryos of *O. dentex* can be successfully hatched at temperature range of 8–14℃, and the salinity range of 0–16psu but not in 32psu. The incubation period of embryos was affected by temperature (31 days at 8℃ and 14 days at 14℃). The salinities range of 0–24psu, however, did not affect the incubation period. The threshold temperature at which embryogenesis ceases was estimated to be 3.4℃. Early stage of *O. dentex* larvae of 15 days after hatching obtained highest survival rate at the rearing in 0–16psu, and the highest growth rates showed at 8 and 16psu. The osmoregulation organ systems in early larval stages might be still not sufficiently developed to encounter the osmoregulatory stress in high salinity environment, and hence, caused the mortality.

5.1. Introduction

Water temperature and salinity are critical abiotic environmental factors that have the greatest effect on the whole life history of fish (Kinne 1963; Fielder et al. 1995; Ostrowski et al. 2001). Especially in the early life stage, since eggs and larvae of fishes are considered. Temperature have been considered as one of the most important environmental factors influencing embryonic development of fish (Bermudes and Ritar 1999; Kamler 2002; Pena et al. 2014). Water temperature can affect hatching rates, larval sizes at hatch, and larval survival and growth (Hart and Purser 1995; Hansen and Falk-Petersen 2001; Akatsu et al. 1983; Garcia-Lopez et al. 2004; Hernandez-Rubio and Figueroa-Lucero 2013). Previous studies showed that development rate of fish embryos varied with temperature: low temperature in the incubation period results in slower developing rate of eggs, and vice versa (Small and Bates 2001; Das 2006). And also, salinity is as one of the important factors that constrains the spawning in fish (Lecomte 2012). Salinity, by influencing physiological state, can affect the embryonic development of fish (Holliday 1969; Blaxter 1988; Rombough 1997; Howell et al. 1998). High mortality in the early stage of embryos of fish when the embryos exposed to extreme salinities have been noticed by Holliday and Jones (1967) and Lee et al. (1981). The fluctuation in these factors can affect the hatching of eggs and the survival and growth fish larvae, and may have substantial effects on future growth and survival (von Westernhagen 1988; Swanson 1996).

The smelts family (Osmeridae), which includes 6 genera and 16 species, is anadromous fishes and distributes in Northern Hemisphere in Atlantic and Pacific Oceans in both freshwater (coastal areas, rivers, streams and lakes) and sea water (Eschmeyer 1998; Nelson 2006). Recently, the smelts family have experienced severe population declines due to destruction of living habitat (e.g. coastal river dam creation), overfishing, and industrial water pollution (Carscadden et al. 2001; Hoff 2004; Mills et al. 2006, O'Gorman et al. 2008, Nii et al. 2010; Enterline et el. 2012; Wood et al. 2012; Chase et al. 2019). Consequently, one of the important species in

the family, rainbow smelt *O. mordax* and *O. eperlanus*, are listed in the 'Least Concern' category in the IUCN red list. Houde (1997) suggested that fish's natural mortality rates are highest in their early life stages. Thus, the timing of spawning, hatching and first feeding may be critical for recruitment success. In response to the declines of the population, the effects of environmental factors on the development of fish eggs and larvae have been studied (e.g. *O. mordax*: Ayer et al. 2005; Fuda et al. 2007; *O. eperlanus*: McCarthy et al. 2019), and regional conservations plan for this species have been developed (Enterline et al. 2012; Verreault et al. 2012).

O. dentex usually lives near Hokkaido's coastal waters and ascends rivers only in the spawning season (Yanagawa 1978). In southern Hokkaido, spawning continues for about a month from late April to late May (Shibata 1950a; Yanagawa 1978). So far, this specie has not been exploited that much. However, due to recent climatic changes, various fishery resources fluctuate (Tian et al., 2014), thus it is necessary to consider using of unused resources such as this species for the stable supply of food. For *O. dentex*, previous studies have existed reporting the embryonic development of this fish (Mihara and Shibata 1940; Nakamura 1948; Shibata 1950b; Yanagawa 1978; Takahashi et al., 2016), but little is known about the relationship between the optimum environment such as temperature and salinity on the embryos and larvae of this species. Studies have also reported that changes in water-temperatures affect fish growth and survival in their early development periods (Edwards and Richardson 2004; Rijnsdorp et al. 2009). Thus, this study seeks to determine the effects of temperature and salinity on hatching success and embryonic period, as well as the influence of salinity on the early life stage of *O. dentex*.

5.2. Materials and Methods

On the night of 29 April and 7 May 2020, mature females and males *O. dentex* were captured by hand or scoop net at the mouth of the Yamazaki River, Yakumo, Hokkaido, Japan. Body length of the male ranged from 217–294 mm, and that of

female was 257–310 mm (Table 5-1). Briefly, the fishes were used for artificial fertilization at the river. Mature eggs and sperm were collected by manually strip-spawning, and fertilization was performed by dry method as previously described by Takahashi et al. (2005). Fertilized eggs (embryo) of *O. dentex* were then incubated in a 2*l* circle shape tank at a temperature approximately of 10°C. Embryonic development was observed with a dissecting micro scope every day until hatching. Hatched larvae were used for the experiment that evaluating the effects of salinities for the larval growth and survival.

5.2.1. Effects of different temperatures on hatching success and embryonic period

For hatching experiment, 27–56 embryos were randomly transferred by pipette to plastic containers (300 m*l* each) filled with 200 m*l* tap water. Incubation temperatures of the embryos were maintained in the incubators set at 8, 10, 12 and 14°C. Experimental set up was displayed in Table 5-1. Twenty percent of water in containers was exchanged daily. At 15:00–16:00 daily, water temperatures, number of dead embryos, and number of hatched larvae were recorded. Hatching percentage were calculated as the percentage of hatched larvae in the treatment. The relationship between temperature and embryonic period of fish were estimated using Réaumur's law model (Brittain 1977; Hamel et al. 1997; Mihelakakis and Yoshimatsu 1998; Yang and Chen 2005) as the following:

$$D = a/(T - b)$$

where D is the mean embryonic period in days, T is the mean incubation temperature, and a, b is the so-called "thermal constant" and "threshold temperature", respectively. The regression was fitted using the non-linear least squares regression procedure (MS-Excel solver routine).

5.2.2. Effects of different salinities on hatching success and embryonic period

In this experiment, 20 embryos were randomly transferred by pipette to 15 plastic containers (300 m*l* each) filled with 200 m*l* of designed salinities water. Experiment was set up with five different salinities of 0, 8, 16, 24 and 32psu, in

Table 5-1. Broodstock sampling and artificial fertilization, body size, eggs size, water temperature and number of eggs observed

Broodstock sampling			TL (mm)		Egg size (mm)	Water temperature (°C)		Egg samples
Site	Year	Date	Female	Male	Diameter (mean ± SD)	Target	Real (mean ± SD)	Number of eggs
Yamazaki River	2020	29 Apr.	278, 293 (n=2)	229 ± 10.8 (n=3)	1.37 ± 0.026 (n=20)	8	8.1 ± 0.46	47
						10	9.9 ± 0.63	41
						12	11.6 ± 1.20	37
						14	13.0 ± 1.86	56
		7 May	290 ± 5.4 (n=4)	289 ± 26.0 (n=4)	1.37 ± 0.026 (n=20)	8	8.0 ± 0.33	30
						10	9.9 ± 0.55	43
						12	12.0 ± 0.58	36
						14	13.8 ± 0.55	27

represent to 0, 25, 50, 75 and 100% sea water, respectively. Three replicates for each treatment. Larvae in all of the treatments were incubated at 10°C. Water was exchanged at rate of 20% daily, and water salinities in each container was checked and adjusted to the designed salinities. At 15:00–16:00, number of hatched larvae (without deformed larvae) and dead embryos were recorded every day. Notochord length (NL) of hatched larvae were measured under stereo-microscope.

5.2.3. Effects of different salinities on survival and growth of the larvae

To determine the effects of salinity on survival and growth of *O. dentex* larvae. Ten newly hatched larvae (with the mean initial notochord length (NL) of 7.2 ± 0.28 mm; n = 10) were randomly stocked in 12 plastic containers (300 m*l* each) filled with 200 m*l* designed salinities water. Experiment was set up with four different salinities of 0, 8, 16 and 24psu in represent to 0, 25, 50 and 75% of full-strength sea water, respectively. Three replicates for each treatment. Larvae in all of the treatments were incubated at 10°C. Water was exchanged 20% daily, water salinities in each container were checked and adjusted to the designed salinity daily. The rotifer *Brachionus plicatilis* were fed daily at the density of 10 ind./m*l*, rotifers were enriched with Super Capsule A1 Powder (Chlorella Industry Co. LTD., Tokyo, Japan) before feeding. Number of dead larvae were counted and then removed from 15:00–16:00 every day. Fifteen days after hatching, all larvae were sampled and measured their notochord length. Growth rate of larvae was calculated using the following:

$$Growth\ rate\ (mm/day) = \frac{final\ length\ (mm) - mean\ initial\ length\ (mm)}{time\ (days)}$$

5.2.4. Statistical analysis

One-way analysis of variance (ANOVA) was used to compare mean among treatments. If statistical differences were found, Tukey's post hoc test were used for

multiple comparisons among means with $\alpha = 0.05$. Percentage data were arcsine transformed to satisfy the ANOVA assumption of normality.

5.3. Results

5.3.1. Effects of different temperatures on hatching success and embryonic period

The egg diameter of each batch was not significantly different (*t-test*, $p = 0.30$). Therefore, the replicate within each temperature setting were pooled. The mean embryonic period (± standard deviation (SD)) and survival rate at 8, 10, 12 and 14°C were 31 ± 0.5 (100%), 21 ± 0.6 (100%), 19 ± 0.6 (89%) and 14 ± 0.2 days (92%), respectively (Fig. 5-1). The survival rates below 10°C (8 and 10°C) were significantly higher than those at higher temperature (12 and 14°C) ($p < 0.05$). The relationship between the mean rearing temperature (T; °C) and the mean embryonic period (D; days) was as follows: $D = 147.3/(T - 3.4)$ ($r^2 = 0.96$, $p < 0.001$, $n = 8$; Fig. 5-2). The threshold temperature at which embryogenesis ceases was estimated to be 3.4°C.

5.3.2. Effects of different salinities on hatching success and embryonic period

The highest hatch (100%) was observed on embryos incubated at 8psu, followed by the embryos maintained at 16psu (98 ± 2.9%; mean ± SD) and freshwater (0psu) (93 ± 7.6%) (Fig. 5-3). Mortality of *O. dentex* embryos incubated at sea water (32psu) started to occurred at 7 days after fertilization (DAF) and 100% of mortality were recorded at 13 DAF. While, the embryos kept in 24psu treatment obtained the lowest hatch (63 ± 29.2%), and was significantly lower than those of 8 and 16psu ($p = 0.02$ and 0.03, respectively). No significant differences between hatching of larvae at 0 and 24psu were detected ($p = 0.59$). Except in 32psu treatment, embryonic period of *O. dentex* incubated at different salinities from other treatments ranged from 22 ± 0.8 to 23 ± 1.0 days. No significant difference was detected between treatments ($p = 0.52$; Fig. 5-4).

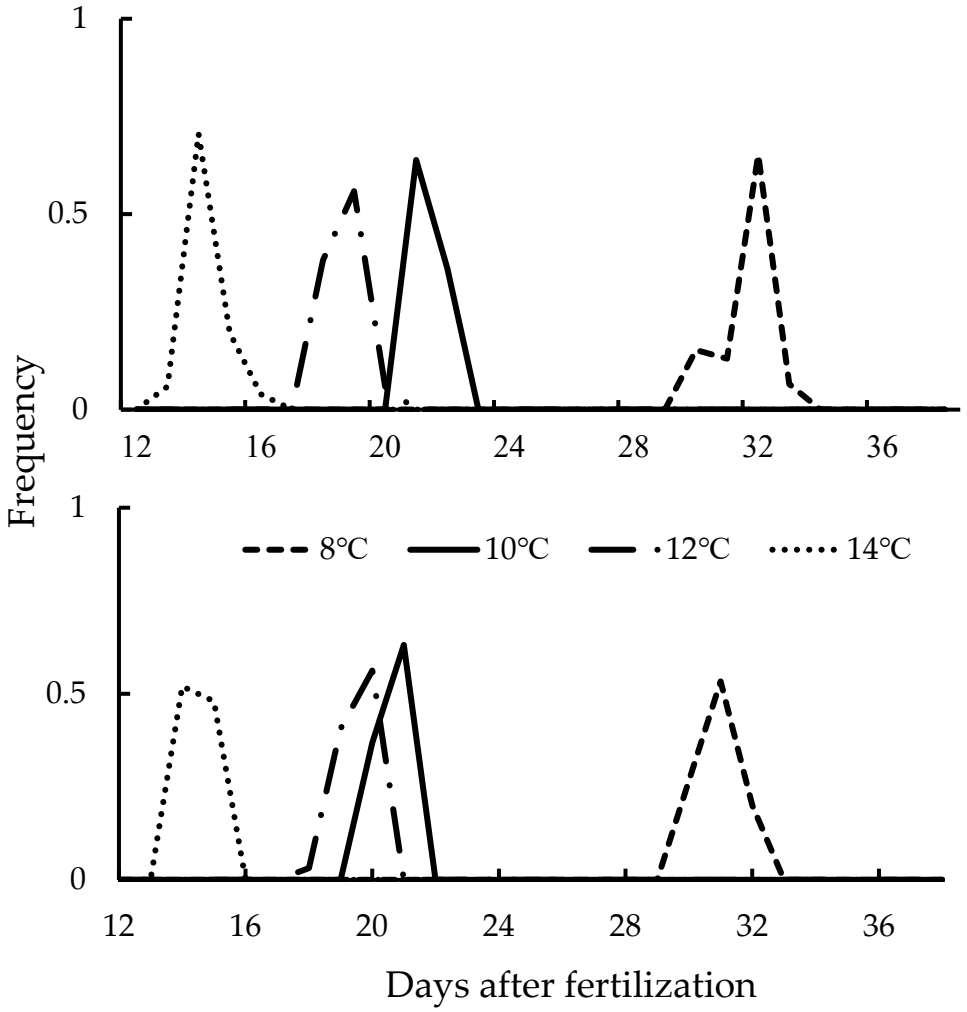


Fig. 5-1. Frequency of the hatching individuals of Pacific rainbow smelt *Osmerus dentex* under the different water temperature conditions (8, 10, 12 and 14ºC).

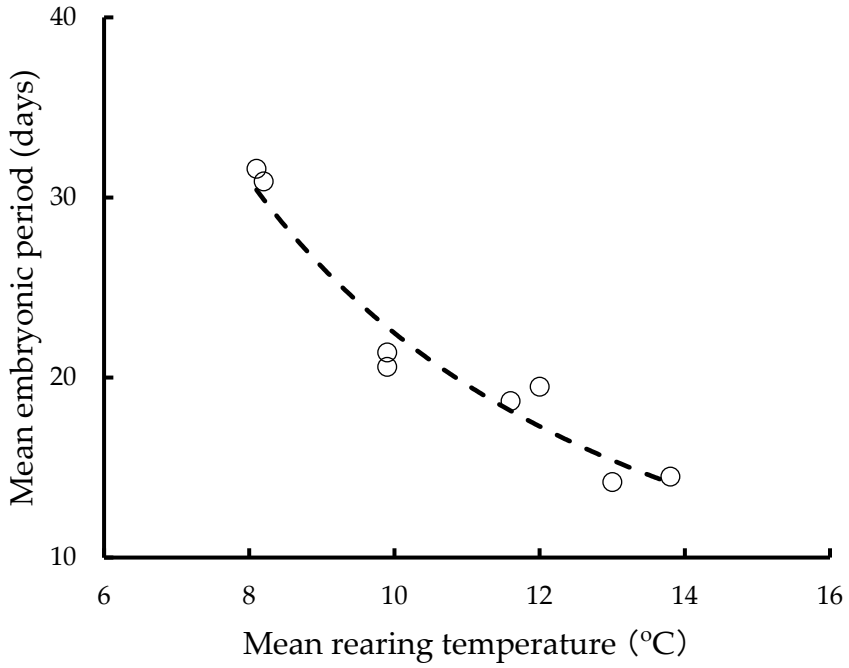


Fig. 5-2. Relationship between mean rearing temperature and the mean embryonic period of Pacific rainbow smelt *O. dentex*.

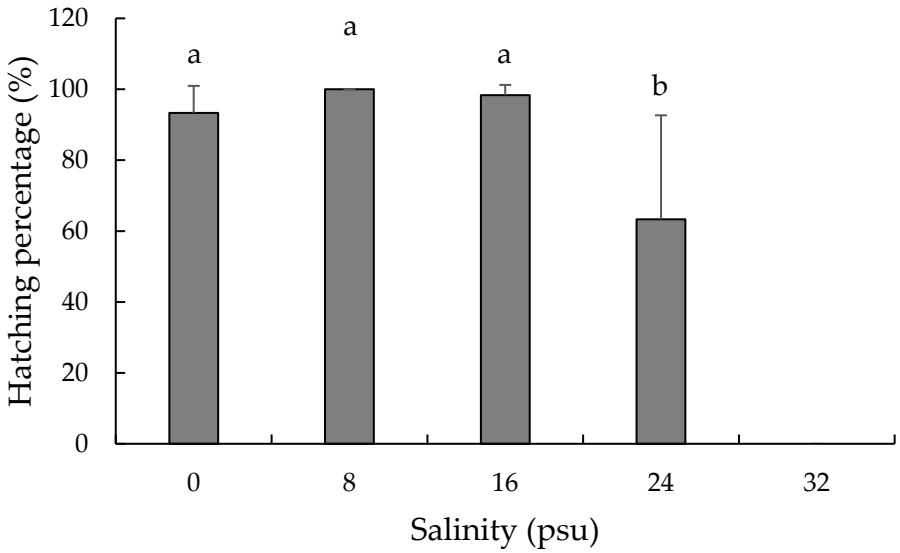


Fig. 5-3. Hatching rate of *O. dentex* embryos under different salinity conditions. Different letters show significant difference at 0.05 level by Tukey's multiple comparisons.

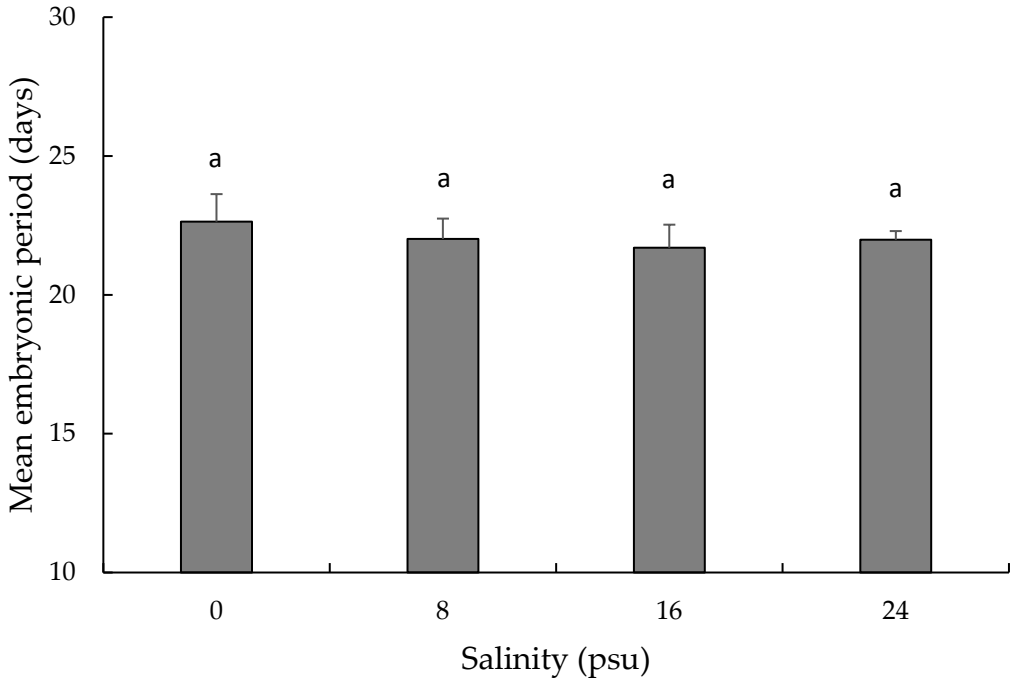


Fig. 5-4. Mean embryonic period of *O. dentex* under different salinity conditions.

5.3.3. Effects of different salinities on survival and growth of the larvae

Survival rate of *O. dentex* larvae cultured at different salinities was showed in Fig. 5-5. Ranges of their survival rate were from 27 ± 5.8 to 67 ± 5.8% (mean ± SD). Survival rate of *O. dentex* larvae stocked at 24psu was significantly lower than the other salinities ($p < 0.05$). The mean growth rate of fish at 15 DAH varied from 0.24–0.31 mm/day (Fig. 5-6). Significant effects of salinities on growth rate of *O. dentex* larvae were detected as growth rate of *O. dentex* reared at 8 and 16psu (0.30 ± 0.014 and 0.31 ± 0.011 mm/day (mean ± SD), respectively) were higher than those at 0 and 24psu (0.24 ± 0.013 and 0.26 ± 0.021, respectively) ($p < 0.01$).

5.4. Discussion

5.4.1. Egg development

This study demonstrated that incubation temperature ranges from 8 to 14°C supported the hatching success of *O. dentex*. The egg incubation period of *O. dentex* decreased with increasing temperature (Fig. 5-2). Embryos of *O. dentex* were successfully hatched at temperature range of 8–14℃. The incubation period of embryos was affected by temperature (31 days at 8℃ and 14 days at 14℃). The threshold temperature at which embryogenesis ceases was estimated to be 3.4℃. Embryos of *O. mordax* were successfully hatched at temperature range of 10–15℃ and their incubation period were 23 and 11 days, respectively (Ayer et al. 2005). For *O. eperlanus*, range of the best temperature was 5–10℃. And the time to first hatch (days after fertilization) and hatching duration were 42 and 10 days at 5℃, and 18 and 7 days at 10℃ (McCarthy et al. 2019). Thus, *O. dentex* seems to be more adapted to the warmer area than both *O. mordax* and *O. eperlanus*. This study is to elucidate the specific distribution of the genus *Osmerus* from the viewpoint of higher temperature adaptation in egg development.

This study demonstrated that incubation salinity ranges from 0 to 16psu supported the hatching success of *O. dentex*. According to McCarthy et al (2019), hatching success of *O. eperlanus* between 0 to 10psu was high (range; 82–96%)

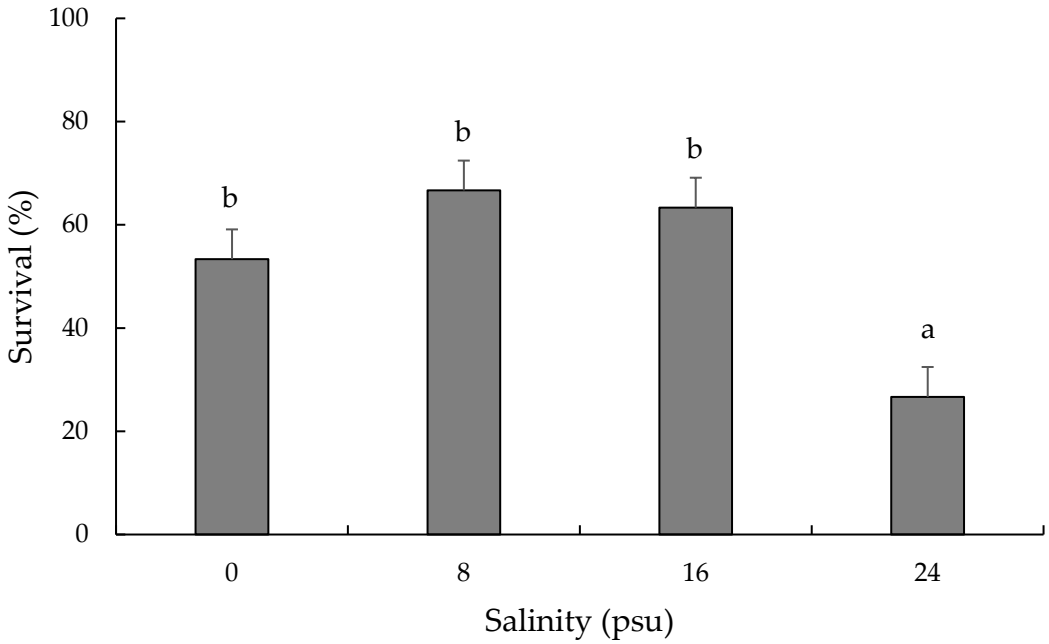


Fig. 5-5. Survival rate of *O. dentex* larvae reared under different salinity conditions.

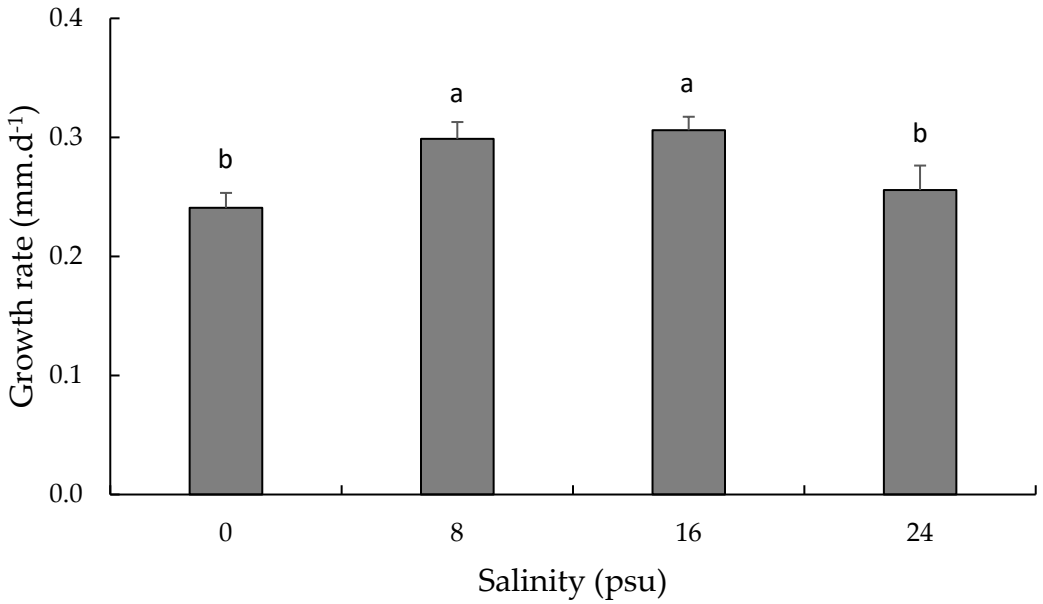


Fig. 5-6. Growth rate of *O. dentex* larvae reared under different salinity conditions.

with a general reduction in hatching success at salinities from over 10 to 20psu with extremely poor (range; 0–17%). Hatching success of *O. mordax* between 0 to 10psu was high (100%) and no hatching occurred at 20psu (Ayer et al. 2005; Fuda et al. 2007). The genus Osmerus can survive in a wide range of salinities as they can distribute in both fresh water and sea water environment. However, evidence showed that high salinities may act as an inhibitor on early life development of the fishes, especially, at the embryonic stages. In the present study showed that the hatching limit is not so different among the three species, being ca. 20psu.

5.4.2. Larval survival and growth

Early stage of *O. dentex* larvae of 15 DAH obtained highest survival rate at the rearing in 0–16psu. According to Holliday (1969), many aspects of the physiology of fish larvae (for instance, the osmotic and ionic concentrations of the body fluids) are influenced by salinity. The response to salinity of fish at different developmental stages will determine the survival of the embryo up to hatching, and the mortalities at specific stages of development. A result from Ayer et al. (2005) showed that *O. mordax* larvae obtained uniformly high survival (> 78%) at all salinities tested (2, 10 and 20psu) after 10 days of culture. This implies that salinity ranges of 2–20psu have no effects on *O. mordax* larvae. However, authors did not examine the effects of higher salinities (> 20psu) on larval survival in the study. Also, the larvae of *O. eperlanus*, survival to first feeding was significantly lower in larvae reared at 15psu when compared to those reared at under 10psu, and no larvae reared at 20psu survived to first feeding (McCarthy et al. 2019). Our studies achieved mostly same results as no significant difference was detected in survival of *O. dentex* at range of 0–16psu. Besides that, our results detected that higher salinity of 24psu significantly reduced the survival of larvae. This might be caused by the osmoregulatory stress (or osmoregulation ability of the larvae). Akielaszek et al. (1985) suggested that osmoregulatory stress may reduce the survival of early stages *O. mordax* larvae. As

mentioned above, osmoregulation ability of the larvae develops as growth, the osmoregulation organ systems in early stages larvae might be still not sufficiently developed to encounter the osmoregulatory stress at high salinities. And hence, cause the mortality.

In this study, growth rates of 0.24–0.31 mm/day were achieved by *O. dentex* larvae. Growth rate of larvae were high at 8 and 16psu. While, the growth rate of larvae reared at 0 and 24psu were significantly lower. The lower growth rate in larvae of *O. dentex* at 0psu might be explained by feeding capacity of the larvae. *O. dentex* larvae at 0psu, in some way, might fed less effective than that at brackish water. This effect had been described by Takahashi et al. (2016), when the author found that *O. dentex* fed better at 11psu sea water than at freshwater. A possible explanation for the lower growth rate in larvae of *O. dentex* at 24psu is energy cost for osmoregulation in larvae. According to Boeuf and Payan (2001) the osmoregulation can require up to 50% of a fish's total energy budget; salinity can change the amount of energy available for body growth by altering the energetic cost for osmotic and ionic regulation. *O. dentex* in this study, when stocked at 24psu, might spent more for energy for osmotic and ionic regulation, hence, caused lower growth rate than that at 8 and 16psu. Furthermore, changes in environmental salinity approaching the physiological tolerance limits of the species are likely to act as a stressor and adversely affect the feeding by influencing the appetite (Gregory and Wood 1999) and the metabolism (Neill et al. 2004) of fish. In this way, the feeding of *O. dentex* larvae reared at salinity of 24 in this study might be affected, therefore, resulting in the low growth rate. However, these explanations are just possibilities, additional research is required to further clarify the effects.

CHAPTER 6. CONCLUSIONS, GENERAL DISCUSSIONS, AND FUTURE RESEARCH

6.1. Conclusions

This study compared the accuracy of age determination of Pacific rainbow smelt *O. dentex* scale and sagittal otolith, and I found that otoliths were a better trait with less error among readers. Many previous studies have considered otolith increments as age traits and examined growth patterns without validating that they are annual increments, but in this study, I confirmed that these are annual increments by examining otolith specimens collected on a perennial basis.

The growth trajectories were similar between both sexes of *O. dentex*, but the biological minimum size of the male was slightly larger than female.

Although the Gompertz growth equation was judged as the best fit model for the growth curves of *O. dentex* by r^2 and AIC values, there was little difference in goodness of fit among Gompertz, logistic, von Bertalanffy, and Richard's growth equations. The reason for this was presumed to be that lower growth rates were not observed at a young age and almost all data were larger than the inflection points of these four growth curves showing the maximum growth rate.

The maximum age and body size of *O. dentex* in Funka Bay and the mouth part of the Yamazaki River were generally lower than those of *O. dentex* collected in the Beaufort Sea off Alaska, Norton Sound, and southeastern Chukchi Sea in the Arctic Ocean form other studies. However, the growth rate in Funka Bay was higher than those of *O. dentex* collected in those areas. The difference might be caused by latitudinal effects, food availability, and photoperiod between areas.

Ontogenetic shift in diet was detected in *O. dentex* in Funka Bay and the mouth part of the Yamazaki River. The smaller sized *O. dentex* (< 156 mm SL and 184 mm TL) fed mainly on Decapoda Natantia, Mysidacea, and Amphipoda Gammaridea, and the larger sized one (≥ 157 mm SL) fed mainly on Pisces

(fishes such as Japanese anchovy *Engraulis japonicus*, walleye pollock *Gadus chalcogrammus* juveniles, and other three demersal fish juveniles). High percentages of empty stomachs in *O. dentex* in Funka Bay and the Yamazaki River (*%VI*=73 and 88, respectively) during April-May were presumed to be caused by low prey requirement during spawning season, the low abundance of walleye pollock juveniles in the environment and the fact that Japanese anchovy was not distributed at all in the low water temperature environment.

Embryos of *O. dentex* were successfully hatched at temperature range of 8-14℃, and the salinity range of 0-16psu but not in 32psu. The incubation period of embryos was affected by temperature (31 days at 8°C and 14 days at 14°C), but not by salinity in range of 0-24psu. The biological zero degree at which embryogenesis ceases was estimated to be 3.4℃, and the cumulative temperature unit was calculated to be 220 ± 25.6 day·℃.

Early stage of *O. dentex* larvae of 15 days after hatching (DAH) obtained highest survival rate at the rearing in 0-16psu, and the highest growth rates showed at 8 and 16psu. The osmoregulation organ systems in early larval stages might be still not sufficiently developed to encounter osmoregulatory stress in a high salinity environment, and hence, cause mortality. It is suggested that an acclimation in *O. dentex* larvae is necessary for survival the larvae into brackish water (may be into estuary and coastal area) until 15 DAH at least.

6.2. General discussions

The three main species of the genus *Osmerus*; *O. mordax*, *O. eperlanus*, and *O. dentex*; distribute widely in fresh and salt water of the northern hemisphere. For more understanding about the genus, comparisons in biological and ecological characteristics among the species together with the Arctic population of *O. dentex* are listed (Table 6-1). *O. dentex* in Japanese waters showed lower in maximum age and body length, but exhibited a higher growth rate with the causes that are considered as latitudinal effects, food availability, and photoperiod (see chapter 3).

Table 6-1. Comparison of some ecological and biological features among *O. dentex*, *O. mordax*, and *O. eperlanus*

Species	Max. age	Max. body length (mm)	Growth perf. index ϕ'	Diet		Envi. temp. (quasimedian)	Temp. at hatching (℃)	Hatching period (day)	Hatching salinity (PSU)	Salinity in larval period (PSU)	Egg diameter (mm)	Body length at hatching (mm)	Larval growth (mm/day)	References
				juvenile and young	adult									
O. mordax (North America, mainly freshwater)	6[5]	259[6]	2.46[3]	Cope-poda[3], Cladocera[2], Amphi-poda[3]	Benthic crustacea[2], Pisces (freshwater). Copepoda[3], Euphausiacea[3], Amphipod[3], Polychaeta[3], (salt water).	7-16 (11.5)[6], 6-18 (12)[1]	10-15[4]	11-23[4]	0-10[4]	2-20[4]	0.86[2]	5.5-6[2], 5[4]	0.6[4]	1) Scott & Crossman (1973), 2) Becker (1983), 3) Buckley (1989), 4) Ayer (2005), 5) Mrnak (2016), 6) Earkins (2021),
O. eperlanus (European fresh and salt water)	7[9]	270[9]	2.32[12]	Copepoda[8], Cladocera[8]	Pisces[10], Apmphipod[10], Mysidacea[10], Isopoda[10], Cladocera[10]	5.5-12[12] (8.8)	5-10[11]	18-42[11]	0-10[11]	<15[11]	0.75-0.9[7]	4.6-6[12]	0.44[7]	7) Sepulveda (1994), 8) Northcote and Hammar (2006), 9) Kottelat and Freyhof (2007), 10) Taal et al. (2014), 11) McCarthy et al. (2019), 12) Fishbase (2021)
O. dentex (Japanese fresh and salt water)	7[13]	310[13]	2.55[13]*	Natantia[13], Copepoda[13], Mysidacea[13], Amphipoda[13]	Pisces[13], Natantia[13], Mysidacea[13], Amphipoda[13], Isopoda[13]	3-15.6[13] (9.5) (Funka Bay)	8-14[13]	14-31[13]	0-16[13]	8-16[13]	1.37[13]	7.2[13]	0.24-0.31[13]	13) This study
O. dentex (fresh and salt water of other areas: Arctic Sea and Russian waters)	10[15]	360[15]	2.14[14]	(No data)	Pisces[14], Natantia[14], Mysidacea[14], Amphopoda[14], Isopoda[14]	−1.6-4.8[12] (1.6)	(No data)	(No data)	(No data)	(No data)	(No data)	(No data)	(No data)	14) Wolotira (1979), 15) Datsky (2017),

* Calculated from total length in cm.

In comparison with *O. mordax* and *O. eperlanus*, the maximum body length of the osmerid fishes showed highest in *O. dentex* inhabited in Arctic Sea and Russian waters (360 mm BL), followed by *O. dentex* in Funka bay (310 mm BL), *O. eperlanus* (270 mm BL), while *O. mordax* exhibited the smallest in maximum size (259 mm BL). This pattern, in relation to the optimal living temperature of the genus, seems to follow the temperature-size rule (Angilitta and Dunham, 2003), which describes the relationship between temperature and body size in nature for ectothermic animals. The rule implies that organisms grow larger in colder environments: *O. mordax* has the highest habitat temperature (10-15°C) and therefore the smallest maximum size.

Growth performance index (ϕ') of *O. eperlanus* showed a smaller value (2.32) than *O. dentex* in Funka Bay (2.55) and *O. mordax* (2.46). The possible explanation may be related to the living temperature. The relationship between temperature and growth performance index among osmerid species was plotted in Fig. 6-1a. Growth performance index was positively correlated with habitat temperature. The exception in the growth performance index of *O. dentex* in Funka Bay may be caused by high food availability. The growth performance index of osmerid species tended to be higher for larger egg diameters, but this was not a sufficiently strong explanation for the relationship between only three species (Fig 6-1b).

Optimum salinity for rearing of *O. dentex* larvae was 8-16, this value was mostly similar to that of *O. eperlanus* (<15psu). While the optimum salinity of *O. mordax* larvae showed a slightly higher value (2-20psu). Species with a greater distance between the freshwater spawning grounds and the high-salinity ocean were expected to have a higher growth rate during the larval stage because of the lower metabolic cost of osmoregulation.

Six species of family Osmeridae were distributed in and around Hokkaido Island, they were surf smelt *Hypomesus japonicus* (Brevoort 1856); Japanese smelt *Hypomesus nipponensis* (McAllister 1963); pond smelt *Hypomesus olidus* (Pallas 1814); capelin *Mallotus villosu*s (Müller 1776); Pacific rainbow smelt *Osmerus dentex* (Steindachner & Kner 1870); and long-finned smelt *Spirinchus lanceolatus* (Hikita

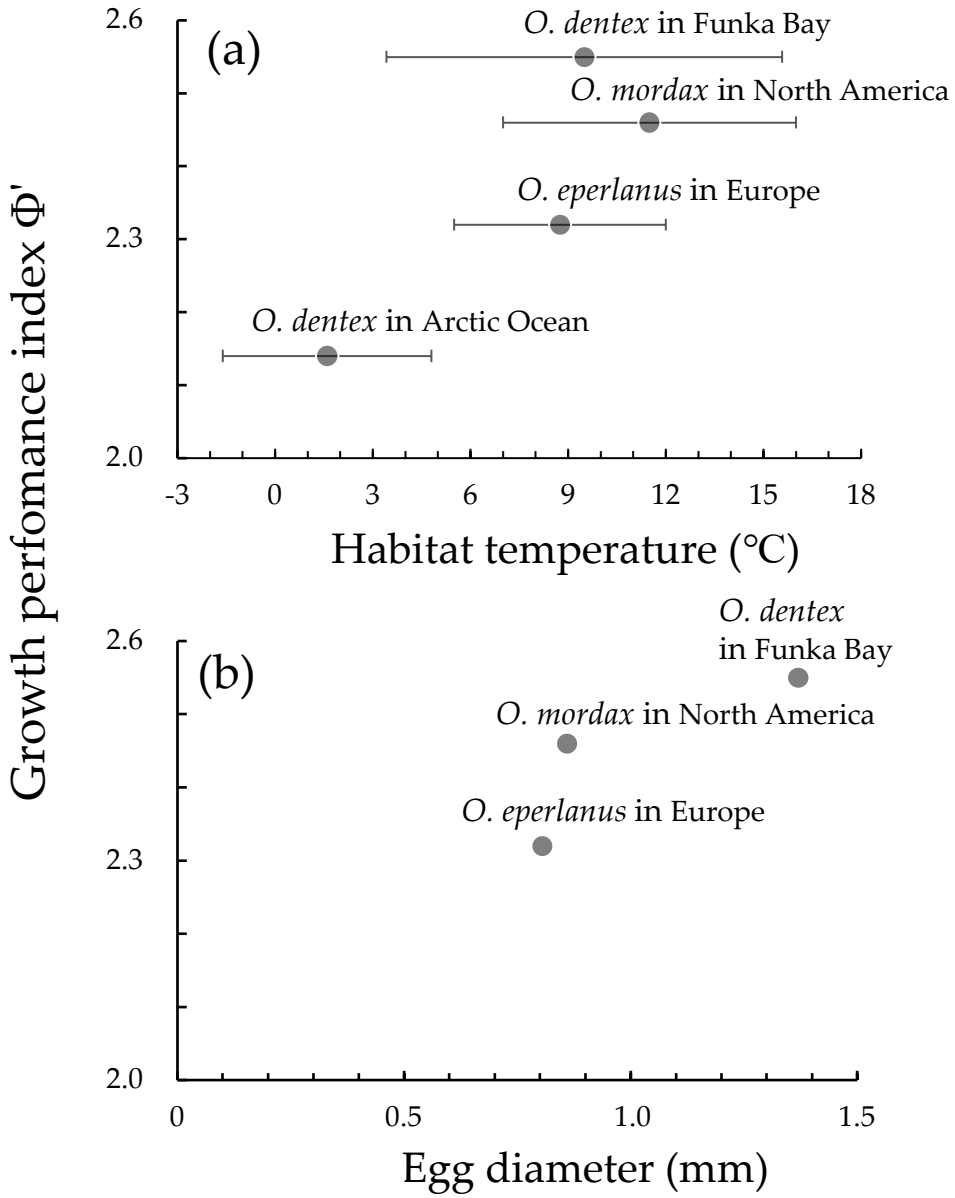


Fig. 6-1. Relationship between growth performance index Φ' and habitat water temperature in quasi-median with range and egg diameter of *Osmerus* spp. Data were shown in Table 6-2.

1913) (Table 6-2). Pacific rainbow smelt, the only species of the genus *Osmerus* recorded in Japan, is distributed mainly in Funka Bay, and the presence of *O. dentex* has also been recorded in coastal areas of the eastern part of Hokkaido and the Sea of Okhotsk. It is interesting that *O. dentex* was mostly absent or rare in the western and northern sides of Hokkaido (Horikawa and Kyushin 1987; Horikawa 1988). This can be explained by the bottom topography of Hokkaido's water: main habitat of *O. dentex* was noticed in the water column shallower than around 70 m (Inokuchi et al. 1997). Funka Bay has a maximum depth of 98 m and a greater area of shallow water (70 m or less) than other bodies of waters in Hokkaido. This geographical feature may be suitable for *O. dentex*. While the 50 m and 80 m depth contours surrounding Hokkaido are narrow (Kido and Ohtani 1981; Kono et al. 2004), and this may be one of the factors that inhibits the living area, and hence, the distribution of *O. dentex* in Hokkaido.

Feeding habits of *O. dentex* can be considered as an important factor that causing the distribution pattern of this species in Hokkaido. As presented in Chapter 4, *O. dentex* fed mainly on fishes such as Japanese anchovy and walleye pollock juveniles. These prey fish species are abundant in Funka Bay as a spawning ground for Japanese anchovies during June-September (Kinoshita 1962) and a nursery ground of walleye pollock through the year (Nakatani and Maeda 1987). Walleye pollock were reported to spawn mainly near the mouth of Funka Bay, most of the eggs are transported into the bay, the larvae and juvenile fish grow in the bay, and then some individuals migrate outside the bay to the Pacific coast of Hokkaido (Maeda et al. 1979; Kawauchi et al. 2011), but some individuals overwinter on the seafloor in the bay until they are one year old (1+) (Maeda et al. 1979). In this study, it was confirmed that walleye pollock juveniles inhabit on the seafloor in Funka Bay where *O. dentex* is distributed year-round and Japanese anchovies inhabit from at least late August to mid-December. Thus, food availability in Funka Bay may be favorite for the growth and surviving of *O. dentex* in comparison with the other waters of

Table 6-2. Comparison of ecological and biological features of Osmerid fishes in Japan

Name (Japanese name)	Scientific name	Distribution	Max. length (cm)	Prey item	Spawning		Period of egg (days)	Egg diameter (mm)	Larval length (mm)*	References
					area	period				
Pacific rainbow smelt, Arctic smelt, toothed smelt (kyuuriuo)	*Osmerus dentex*	Artic Ocean (from White Sea, Russia to Beaufort Sea, Alaska USA)[4], Hokkaido Japan[3,4,6], Wonsan Korea[4,5]	36[1], **31[6]**	Pisces[2,4,6], Natantia[2,4,6], Copepoda[2,4,6], Amphipoda[2,4,6]	River[6]	Apr.-June[3,5]	**14-31 (8.0-13.8°C)[6]**	0.76-1.21[5], **1.37±0.026[6]**	7.2[6]	1) Wolotira et al. (1979), 2) Haldorson and Craig (1984), 3) Horikawa (1988), 4) Mutoh (2003a), 5) Kottelat and Freyhof (2007), **6) This study**
long-finned smelt (shishamo)	*Spirinchus lanceolatus*	southeastern Hokkaido (42-45°N)[7]	18[7]	Polychaeta[9], Isopoda[9], Amphipoda[9]	River[7]	Oct.-Nov.[7]	35-100 (3-10°C)[8]	1.4[8]	8-9[8]	7) Mori (2003), 8) Mizuno et al. (2004), 9) Shebanova et al. (2011)
surf smelt (chika)	*Hypomesus japonicus*	Coast of North America (Long Beach-California)[13], Western Pacific Ocean (Kamchatka-Korea)[13], Northern Japan[12,13], Russian coast of Sea of Japan[12,13]	25.4[13]	Cladocera[13], Mysidacea[13], Copepoda[13], Amphipoda[13], Gastropoda[13]	Coast[12], Beach1[2]	Mar.-May[11] (Otsuchi Bay), Apr.-May[12] (Hokkaido)	22-25 (8-10°C)[10], 15-21 (10-17°C)[11]	1.04-1.26[12]	6-6.5[10]	10) Shadrin (1989), 11) Hirose and Kawaguchi (1998), 12) Mutoh (2003b), 13) Fishbase (2021),
Japanese smelt (wakasagi)	*Hypomesus nipponensis*	Japan to the Korean Peninsula[17]	17[17]	Rotatoria[16], Cladocera[16], Copepoda[16]	River[17]	Feb. (west. Japan)[17], Mar.-Apr. (Tohoku region)[16], Apr.-June (Hokkaido)[15,18]	12-38 (7-15°C)[17], 7.1 (16.5°C)[14]	1.0[17], 0.67-0.84, 0.97[14]	4-7[17], 4.05[14]	14) Han et al. (1996), 15) Asami (2004), 16) Chang et al. (2005), 17) Asami (2003), 18) Mizuno et al. (2013)
pond smelt (Ishikari-wakasagi)	*Hypomesus olidus*	Arctic Ocean[22], Northern Pacific Ocean[22], Coastal waters of European and Siberian shores of Artic Ocean[22]	20[32]	Copepoda[19], Cladocera[19], Insecta[19], Algae[19], Rotatoria[19]	Stream[22], Pond[22], River	Apr.-May[22]	14-17 (11-12°C)[21], 11 (11-15°C)[22], 20-30 (7.5-9.5°C)[20], 15-21 (10-17°C)[20],	0.8-0.9[21], 0.95[22]	5[21], 4-5[22], 6	19) Sato (1951), 20) Hamada (1961), 21) Yamada (1963), 22) Morrow (1980)
capelin (Karafuto-shishamo)	*Mallotus villosus*	Arctic Sea[32], Northern Pacific Ocean[32], Okhotsk Sea[32], Northern Atlantic Ocean[32]	23[31]	Amphipod[30], Copepoda[30], Euphausiacea[30], Cladocera[30], Mysidacea[30]	Coast[24], Beach[31]	Sep.-Oct[24].	20-80 (2-7°C)[27], 30-50 (2.8-5°C)[25], 23.6-12.7 (5-15°C)[32]	1.2[32], 0.98-1.27[23], 0.6-0.8[28],	7.55[27], 4.8-7.5[32], 5.1-6.6[28], 5.0-5.9[29]	23) Fridriksson and Timmerman (1951), 24) Clemen and Wilby (1961), 25) Saetre and Gjosaeter (1975), 26) Pepin et al. (1992), 27) Gjosaeter and Gjosaeter (1986), 28) Chamber and Leggett (1996), 29) Purchase (2018), 30) Gronkjaer et al. (2019), 31) FAO (2021), 32) Fishbase (2021),

*: body length at hatching.

Hokkaido.

Some ecological and biological features of osmerid fishes in Japanese water were compared in Table 6.2. The noticeable characteristic of *O. dentex* is larger body size than the other five species. While most of the fishes have the maximum size < 25 cm, the maximum size of *O. dentex* is 1.5–2 fold larger than the others. With the regarding to the feeding habits, *O. dentex* is the only species that fed mainly on fishes. This feature is probably the reason causing the prominent size of *O. dentex* in compare with the other species in the family in Japan.

Another characteristic feature of *O. dentex* in Funka Bay is that spawning takes place in river close to the estuary, where salinity is low, and the first feeding stage larvae are quickly recruited in brackish water (mainly in coastal areas around the estuary) and begin to feed. There are no data for the Yamazaki River to show whether zooplankton abundance is higher in the river or around the mouth in the sea, but the fluctuations of water volume, water temperature and food abundance are probably more stable in the sea than in the river. The egg duration of *O. dentex* is shorter (14-31 days) than that of the long-finned (shihamo) smelt *S. lanceolatus* (35-100 days), which also uses the river near the mouth of the Yamazaki River as a spawning ground in autumn and winter, so the risk of egg predation in the river would be lower. Therefore, I consider that the relatively high abundance of *O. dentex* in Funka Bay and the Yamazaki River is due to the fact that the production ecology of *O. dentex* matches this special and unique environment. These two species are characterized by a larger egg diameter and larger hatchlings than other Osmerid species. *H. japonicus* spawns in the surf zone around the mouth of the Yamasaki River in spring, and larvae of this species are distributed at the same time as *O. dentex* larvae that drift

downstream (K. Inokuchi and T. Takatsu, unpublished data). The morphologies of *H. japonicus* and *O. dentex* larvae are very similar, and no method of identification between them from external morphology has been found. The diet of these two morphologically similar species is naturally likely to be similar, and they use the same habitat during the early life stages when survival rates are low. On the other hand, *S. lanceolatus* also spends its larval stage in the surf zone near the mouth of the Yamazaki River, but occurs earlier than the previous two species, around February. The larvae of *S. lanceolatus* do not differ morphologically from those of the two species, but can be identified by their body length because of the difference in the time of appearance. *H. nipponensis* inhabiting Funka Bay is thought to migrate upstream to spawn in the surrounding rivers, but the habitat of the larvae is not known at present. In the trawl sampling in Funka Bay, where the present study was carried out, immature and adult stage individuals of four species, *O. dentex, S. lanceolatus, H. japonicus* and *H. nipponensis,* were collected simultaneously. Therefore, at least four species of osmerid fishes in Funka Bay and its adjacent rivers maintain their species by using common water areas during feeding period, although their spawning sites (egg habitats) and spawning periods are different. The morphological similarity and the common habitat usage of the four species makes them interesting targets for research into the process of species differentiation.

6.3. Future research

Although, the age and growth of *O. dentex* in Funka Bay and the mouth of the Yamazaki River have been estimated in this study. However, the continuing study to increase the knowledge about the variation in age and growth of *O. dentex* year by year is necessary. Similarly, further study about the shift of feeding habit year by

year is also essential.

The growth rate of *O. dentex* is implied to be affected by latitudinal effects, but the specific underlying factors are not clear. To clarify and increase the knowledges of these effects, further studies on this subject should aim at identifying the roles of the underlying factors. Even now, no statistics on the catches, let alone the abundance of this species, have been collected. The abundance of *O. dentex* collected by quantitative bottom trawl sampling in Funka Bay has been decreasing in recent years (T. Takatsu, unpublished data). To elucidate the mechanism of population fluctuation of *O. dentex*, it will be necessary to clarify the early life ecology of this species, which has the greatest influence on population fluctuation, and to investigate the long-term environmental changes in the Yamazaki River, the main spawning ground of this species.

To enhance stock enhancement in culture-based fisheries of *O. dentex* as well as other osmerid fishes, beside temperature and salinity, the effects of other environmental factors such as pH, photoperiod, feed and feeding regimes on embryonic and larval development be studied to develop the hatchery technology for seed releasing.

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