HOKKAIDO UNIVERSITY

Title	A study on swimming behaviors of larval and juvenile Pacific cod Gadus macrocephalus in relation to temperature and food availability
Author(s)	李, 哲
Degree Grantor	北海道大学
Degree Name	博士(水産科学)
Dissertation Number	甲第12856号
Issue Date	2017-09-25
DOI	https://doi.org/10.14943/doctoral.k12856
Doc URL	https://hdl.handle.net/2115/87560
Type	doctoral thesis
File Information	Zhe_Li.pdf

Hokkaido University Collection of Scholarly and Academic Papers : HUSCAP

A study on swimming behaviors of larval and juvenile Pacific cod *Gadus macrocephalus* in relation to temperature and food availability

（異なる餌条件と水温におけるマダラ仔稚魚の遊泳行動に関する研究）

北海道大学大学院水産科学院

海洋生物資源科学専攻

Graduate School of Fisheries Sciences

Division of Marine Bioresource and

Environmental Science

李　哲

Zhe Li

2017（平成 29 年）

Abstract

Pacific cod *Gadus macrocephalus* is an important fish species in fishery resource and marine ecosystem in the Northern Pacific Ocean. In Mutsu Bay Japan, cod larvae potentially experience complex thermal conditions and temporary food absence during pelagic life stages, due to varied hatching locations and uneven prey mass distribution. After settlement, juvenile (age-0) cod are transported to the area with drastic changes in temperature and may also suffer temporary food shortage resulted from separations from prey under thermal extremes. Little is known about the relationship between their behavioral responses and the environmental variables (*i.e.* varying temperatures and prey availability), despite its critical roles of in growth, survival and recruitment of this species.

The objective of this study was to clarify the effects of temperature and recent feeding history on vertical distribution and swimming activity of larvae and age-0 juveniles of Pacific cod. Vertical distribution and swimming activity were tested in simulated (normal and reversed) temperature gradients with two ranges (4–8°C and 8–12°C) and at cold, moderate and warm temperatures (4, 8 and 12°C). Larvae were tested at two exogenous feeding stages: young (14–17 days after hatching [dah]) and old (28 and 29 dah). All the fish were either well fed (WF) or food-deprived (FD) for 24h.

Most young maintained upper distribution and old were distributed lower in the temperature gradients, regardless of temperature or recent feeding history. Swimming activity of young larvae tended to increase with temperature, regardless of recent

feeding history. Swimming activity of old larvae was independent of temperature and significantly reduced when larvae were deprived of food. Juvenile cod showed varied responses to the temperature gradients based on recent feeding history. WF juveniles accessed to both the cold and warm temperatures, while FD juveniles preferred the moderate temperature. Swimming activity of WF juveniles was significantly higher at 12°C than those similar ones at 4 and 8°C. Swimming activity of FD juveniles was significantly lower at 4°C than those similar ones at 8 and 12°C.

Vertical distributions may be alternatively dominated by negative and positive geotaxis in cod larvae. In warm conditions, the young larvae are suggested to suffer higher starvation risk than the old larvae, because the latter can save energy by reducing swimming activity. Age-0 juveniles are suggested to have more flexible responses to varying temperatures and prey availability, compared to cod larvae. WF juveniles may utilize increased swimming activity in warm temperatures to improve feeding opportunity and growth rate. They appeared to be able to adapt to the cold temperature. FD juveniles might balance energy expenditure and substantial swimming activity in the moderate temperature

In conclusion, behavioral responses of cod larvae to the environmental variables were less flexible that those of age-0 juvenile cod possessing ability to regulate thermal experience and swimming activity based on recent feeding. In warm conditions, the young larvae are expected to be more susceptible to temporary food shortage compared with older larvae, and age-0 juveniles are expected to have stronger environmental resistance compared to the cod larvae.

Table of Contents

Abstract ii

Table of Contents iv

List of Tables vi

List of Figures vii

Acknowledgements viii

Chapter 1 General introduction 1

1.1 Ecological and biological traits on Pacific cod 1

1.2 Vertical distribution and swimming activity 3

1.3 Study background 4

1.4 Objectives and hypotheses 6

Chapter 2 Vertical movement and swimming activity of Pacific cod larvae *Gadus macrocephalus* in relation to food availability and temperature 8

2.1 Introduction 8

2.2 Materials and methods 11

2.2.1 Eggs collection and larvae rearing 11

2.2.2 Vertical distribution of cod larvae 12

2.2.3 Swimming activity of cod larvae 14

2.2.4 Data analysis 15

2.3 Results 16

2.3.1 Vertical distribution of fish larvae 16

2.3.2 Swimming behavior of fish larvae 18

2.4 Discussion 21

Chapter 3 Vertical movement and swimming activity of age-0 juvenile Pacific cod *Gadus macrocephalus* in relation to food availability and temperature 26

3.1 Introduction 26

3.2 Materials and methods 28

3.2.1 Fish rearing 28

3.2.2 Vertical distribution of age-0 cod 29

3.2.3 Swimming activity of age-0 cod 30

3.2.4 Data analysis 30

3.3 Results 31

3.4 Discussion 34
Chapter 4 General Discussion 39
References 43

List of Tables

Table 2.1 Descriptions of change in direction and change in position of cod larvae .. 15
Table 2.2 Depth-dependent temperatures in five thermal patterns in larval trial 16
Table 3.1 Depth-dependent temperatures in five thermal pattern in juvenile trial 31

List of Figures

Figure 1.1 A diagram of study area.....5
Figure 2.1 A diagram of plexiglass tanks for vertical distribution of cod larvae. 13
Figure 2.2 A diagram of horizontal cylindrical tank for swimming activity of cod larvae.....15
Figure 2.3 Percentages of young larvae occurrences in the five thermal patterns.....17
Figure 2.4 Percentages of old larvae occurrences in the five thermal patterns.....18
Figure 2.5 Swimming activities of young larvae.....19
Figure 2.6 Swimming activities of old larvae.....20
Figure 3.1 Depths of age-0 cod in the five thermal patterns.....32
Figure 3.2 Percentages of age-0 cod occurrences in the five thermal patterns.....33
Figure 3.3 Swimming activity of age-0 cod.....34

Acknowledgements

During all my studying life in Hokkaido University, I was so lucky that I ever had three supervisors: Prof. Yasunori Sakurai, Prof. Yutaka Watanuki and Associate Prof. Orio Yamamura.

First, I express sincere gratitude to Prof. Sakurai for his patience and continuous support. Although I failed in experiments a few times, he never blamed me but tried his best to seek more chances for me. Even when he retired, he was still caring about my experiments. I will always be grateful to him.

I would also like to dedicate special thanks to Prof. Watanuki for his instructions and inspiration. As a student without much talent, I had not noted the importance of logic in scientific research until he taught me to draw procedure diagram less than one month before the master's oral defense. When I was confined in stereotype of research, his incisive questions enlightened me again.

I wish to express sincere appreciation to Associate Prof. Yamamura for his generous help with my dissertation manuscript and research funding report without hesitation. Also, I deeply appreciate his devotion to the laboratory.

Special and deep thanks go to Assistant Prof. Jun Yamamoto for his broad help and earnest instruction at all times and all affairs. Without his help, I could not have completed all the studies successfully.

To Assistant Prof. Mitsuhiro Nakaya, I feel that all appreciation words are eclipsed by his great help for me. Or I prefer to say that great grace does not thank. His diligence,

earnest and action orientation will always drive me to go forward in the rest of my life.

Heartfelt appreciation goes to Prof. Tetsuya Takatsu for his useful comments and advice on the manuscript.

I would like to thank the Wakinosawa Fishery Association and the fishermen in Furube for providing great quality Pacific cod eggs and capturing healthy Pacific cod juveniles, respectively.

I am grateful to Sasakawa Scientific Research Grant from the Japan Science Society for offering substantial funding to a part of the research.

Special and genuine thanks to two friends, Naizheng Yan and Weifeng Gang for their assistance with fish rearing and experiments.

Special thanks also go to Dr. Yumi Kobayasi for her useful advice when I got stuck, and Dr. Takanori Horimoto for helping me to apply for the Sasakawa Scientific Research Grant from the Japan Science Society.

Lastly and personally, I would like to thank to the Uniqlo CO. LTD. for the thick and comfortable jogger pants ensuring me to be in a good condition during the experimental period in the cold winter.

Chapter 1

General introduction

1.1 Ecological and biological traits of Pacific cod

Pacific cod *Gadus macrocephalus* is an ecologically and commercially important marine fish species widely distributed along the continent shelves of the North Pacific Ocean (Alderdice and Forrester, 1971; Laurel et al., 2007). In Asian coastal waters, this species is distributed from the Gulf of Anadyr southward to the southern end of the Korean Peninsula and to the northern Yellow Sea (Bakkala et al., 1984). In the northern Japan, population of Pacific cod is divided into three subpopulations: the stock in the Sea of Japan, the stock around Southern Hokkaido, and the stock in the Northeastern Japan (Kanno et al., 2001). The female adults spawn demersal eggs once a year from December to February (Sakurai and Hattori, 1996). After hatching, yolk-sac larvae actively swim upward and inhabit depths at 30–45 m in Mutsu Bay, Japan (Takatsu et al., 2002; Hurst et al., 2009; Li et al., 2015). After yolk resorption, larvae inhabit in pelagic waters ranging 15–45 m for 4–5 months in the bay (Takatsu et al., 2002; Sakurai, 2007). During the pelagic life, preflexion larvae (from complement of yolk resorption to start of notochord flexion, 6–10mm in standard length [SL]) display strong surface orientation, whereas postflexion larvae (from complement of notochord flexion to start of metamorphosis, 15–18mm in SL) are expected to undergo diel vertical migration (Hurst et al., 2009). This expectation is consistent with the field survey conducted by

Boehlert et al. (1985) reporting that Pacific cod larvae are most abundant at 20–30 m depths in the daytime and >50 m depths at night in summer off the Oregon coast, USA.

Larvae >25mm SL transform into juveniles who will still dwell in pelagic waters (Takatsu et al., 1995) until SL exceeds 35mm that pelagic juveniles commence to settlement into demersal environments (Strasburger et al., 2014). This habitat transition completes in June in Mutsu Bay (Takatsu et al., 2001) and in July in the Gulf of Alaska (Laurel et al., 2007) and eastern Bering Sea (Strasburger et al., 2014). Post-settled juveniles (age-0) inhabit over a broad range of depths from 3–80m in different nursery areas (Laurel et al., 2009; Hurst et al.,2012; Moss et al., 2015; Hurst et al., 2015). They avoid high light intensity and cold waters as low as 3°C (Davis and Ottmar, 2009).

It has been well known that environmental conditions, especially temperature and prey availability are the most important factors for early survival and recruitment of marine fishes (Bailey, 2000; Beaugrand et al., 2003; Platt et al., 2003). The question that at which life stage recruitment is determined has still been controversial in fishery oceanography, which is roughly summarized that environmental factors act in various life stages among fish species and climate regimes (Bailey et al., 2005; Houde, 2008). The “critical period hypothesis” proposes that the year class strength is determined by prey availability for first-feeding larvae (Hjort, 1914). Meanwhile, juvenile stage, in particular the first summer life has been considered to be another “critical period” in fish productivity and raised great interest of fishery biologists (e.g., Bailey, 2000; Bailey et al., 2005; Moss et al., 2009; Hurst et al., 2015). Because either fish habitat transition or prey species transition is likely to fail to satisfy the stage-specific

requirements for growth and survival of juvenile fish (Moss et al., 2009; Nakatani et al., 2003). In my dissertation, it has been assumed that the significances of larval and juvenile periods are not mutually exclusive, but is complementally each other for recruitment process of fishery stocks. Young cod larvae (14–17 dah) had ended the first-feeding stage and completely established exogenous feeding, corresponding to stage 7–8 of Atlantic cod *Gadus morhua* larvae reared at 5°C; old cod larvae (28–29 dah) were in the late larval stage and approaching metamorphosis, corresponding to stage 9–10 of the Atlantic cod larvae (Ellertsen et al., 1980; von herbing et al., 1996; Otterlei et al., 1999; Vollset et al., 2013). In the present study, "age-0 cod" refers to juvenile Pacific cod in the first year of life stage with SL>35mm, which are either in their way of settlement or have just completed settlement.

1.2 Vertical distribution and swimming activity

The issue of vertical distribution of cold water marine fishes has been extensively studied in relation to multiple environment factors, such as temperature, light and prey availability, owing to its direct implications for dispersal, growth and survival in larval and juvenile stages (Miller, 2007; Vikebø et al., 2007). Although they are often considered immobile, fish larvae can acquire locomotory ability very soon after hatching (Clark et al., 2005), and have potential to adjust their vertical positions based on stage-specific preferences (e.g. Olla and Davis, 1990; Vollset et al., 2009). Juvenile fish have stronger swimming ability and can select a preferred habitat based on individual energetic storage (Sogard and Olla; 1996; Breau et al., 2011).

Since most fish larvae do not swim continuously (von Herbing, 2002), swimming activity refers to swimming events per unit time, for instance, change in direction and change in position per minute (Colton and Hurst, 2010). Swimming activity is associated with recent feeding history (Jordaan and Brown, 2003) and represents both encounter probability with prey and evasion ability from predators (Letcher and Rice, 1997; Fiksen and Jørgensen, 2011). Although Ottmar and Hurst (2012) have used the term "swimming activity" to represent swimming speeds in juvenile fish, "swimming activity" was defined as frequency of swimming events in this dissertation. On the other hand, swimming ability has been widely used to present swimming speeds (velocities), and it increases with temperature and body size in larval and juvenile fish (von Herbing, 2002; Ottmar and Hurst, 2012).

1.3 Study background

Mutsu Bay is one of the most important known spawning and nursery grounds of Pacific cod in the North Honshu, Japan (Fig. 1.1) and nearly to the southern limit of this species. A part of the Tsugaru Warm Current flows into the bay, leading to relatively warm temperatures at the bay mouth and cold temperatures in the inner bay (Takatsu et al., 2001 and 2002). Cod larvae in this bay are probably exposed to various temperatures, because of spatio-temporal variety in hatching. In addition, they are transported by the warm current from the bay mouth to the inner bay, experiencing a considerable decrease in temperature (Takatsu et al., 2002). After settlement, age-0 juvenile cod are thought to migrate out of Mutsu Bay (Takatsu et al., 2001) and are transported to the east side

of the Tsugaru Strait in Southern Hokkaido (Kanno et al., 2011). In this area, they are exposed to dramatic fluctuations in thermal conditions as a result of the confluence of warm and cold water masses from the Tsugaru Warm Current and the cold Oyashio Current (Sakurai, 2007; Fig. 1.1).

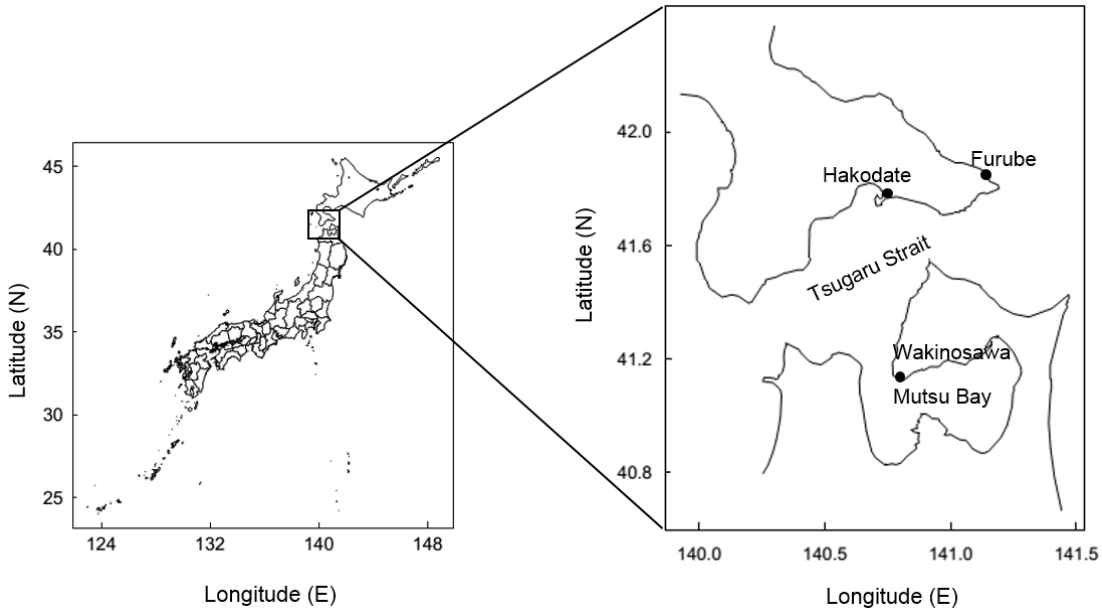

Fig. 1.1 Geographical positions of Mutsu Bay and the eastern side of the Tsugaru Strait in Japan.

Pacific cod larvae and juveniles need to cope with variable thermal environments in Mutsu Bay and on the east side of Tsugaru Strait, respectively. Additionally, cod larvae may hatch in varied locations in the bay and individuals hatching at the bay mouth are transported to the inner bay. Therefore, cod larvae may experience short-term food absence because prey patches are not homogenous in natural conditions (Letcher and Rice, 1997). Similarly, age-0 juvenile cod may suffer prey deficiency in both extreme warm or cold conditions (Sakurai, 2007). Thereby, starvation risk is very

likely to occur to larval and age-0 juvenile cod in these areas, and the resultant mass mortality may seriously affect the population (Houde, 2008). For example, the dramatic decreases in commercial catches of this species in Mutsu Bay in the early 1990s were due to poor recruitment during the warm regime initiated in the late 1980s (Sakurai, 2007).

Under such complex natural conditions as mentioned above, surprisingly, very little is known about the effects of theses environmental variables on Pacific cod, in particular their behavioral mechanism. Laurel et al. (2011) examined the interaction of temperature (3 and 8°C) and prey density (four conditions) on growth and survival in cod larvae, but they did not focus on larval behaviors. Furthermore, previous studies relating larval and juvenile behaviors to prey availability are often conducted in a fixed temperature (e.g. Puvanendran and Brown, 1999; Moberg et al., 2011; Illing et al., in press). Therefore, behavioral studies on this species are indispensable to be conducted in various temperatures and prey availability.

1.4 Objectives and hypotheses

In field conditions, it takes several years or even decades to investigate the relationship between temperature and fish recruitment, and it is also difficult to verify the roles of temperature and short-term food shortage in behavioral responses of fish during early life history. However, controlled experimental conditions make these intentions possible and eliminate other unnecessary factors such as light level. These results can not only improve our knowledge of behavioral mechanisms of this species

but also assist us in forecasting the recruitment dynamics of this species in these areas.

The objective of the present study was to examine the behavioral responses (vertical movements and swimming activity) of larval and juvenile Pacific cod to varied temperatures and short-term food deprivation under experimental conditions. First, I tested the vertical distribution and swimming activity of cod larvae at two feeding stages in "warm" and "cold" conditions (**Chapter 2**). The cod larvae were hatched with artificially fertilized eggs from adults in Mutsu Bay and reared in laboratory. Second, I tested the same items of age-0 cod in the same conditions (**Chapter 3**). The juveniles were captured offshore the Furube on the east side of the Tsugaru Strait.

I expected that both larval and juvenile cod that had experienced short-term food deprivation would migrate towards cold waters and reduce swimming activity in warm waters in order to save energy.

Chapter 2

Effects of food deprivation on vertical movement and swimming activity of Pacific cod larvae *Gadus macrocephalus* in varying temperatures

2.1 Introduction

Fluctuations in recruitment and abundance of marine fish species are highly driven by changes in ocean conditions (Perry et al., 2005; Busby et al., 2014), primarily during early life stages (Houde, 1987). For example, spatial-temporal variations in temperature and zooplankton abundance have been found to impact recruitment success of commercially important fish species (Coyle et al., 2011; Hunt et al., 2011; Beaugrand et al., 2003). Temperature influences larval survival through growth rate, stage duration (Pepin, 1991) and dispersal (O'Connor et al., 2007). In the long run, a warm condition has been supposed to improve larval growth rate only when prey abundance is sufficient to support their physiological requirements (Houde, 1989). Otherwise, a warm temperature may elevate metabolic rates and starvation risks in fish larvae (Laurel et al., 2011; Fouzai et al., 2015). Zooplanktons are the main food resources of fish larvae (Theilacker et al., 1996) and limited zooplankton abundance may cause increase in starvation mortality in fish larvae (Cushing, 1990; Bochdansky et al., 2005).

Vertical distribution largely affects thermal experience, feeding opportunity, growth and survival in fish larvae (Fiksen et al., 2007). Thus, fish larvae select preferred

temperature and prey availability that satisfy stage-specific growth and survival requirements by adjusting vertical distribution as ontogeny (Grønkjær and Wieland, 1997; Huwer et al., 2011; Fouzai et al. 2015). Laboratory studies on larval Atlantic herring *Clupea harengus* and Atlantic cod have indicated that temperature and light may play more crucial roles in vertical distribution than a short-term food deprivation in temperature gradients (Catalán et al., 2011; Vollset et al., 2013). In either study, however, the 16-h time period for food deprivation may be not long enough to induce a remarkable difference in vertical distribution of the larvae tested (Jordaan and Brown, 2003). Thus, a longer duration for food deprivation is supposed to be essential, allowing cold-water fish larvae to substantially digest to a certain starvation threshold, over which differential vertical movements will be triggered.

Swimming activity represents a potential ability to locate and approach to prey patches (Letcher and Rice, 1997; Colton and Hurst, 2010), and is closely associated with feeding opportunity (Fiksen and Jørgensen, 2011). When temporarily deprived of food, fish larvae display lower swimming activity relative to those fed constantly well (Skiftesvik, 1992; Jordaan and Brown, 2003). This lower swimming activity has been considered a behavioral response in order to decrease predation mortality and save energy. Furthermore, Larval swimming activity has been compared in various prey densities, but only in single temperatures (e.g., Munk 1995; Georgalas et al. 2007; Andrade et al. 2011). Ignorance of temperature may mislead us into understanding the relationship between swimming activity and larval survival, and even recruitment dynamics under prevalent changing ocean conditions.

Pacific cod *Gadus macrocephalus* is an ecologically and commercially important marine fish species distributed along the continental shelves of the North Pacific Ocean (Alderdice and Forrester, 1971; Laurel et al., 2007). In Asian coastal waters, this species utilizes Mutsu Bay as one of the major spawning grounds in the Northern Japan. This bay is characterized by a horizontal coexistence of warm and cold temperatures at the bay mouth and in the inner bay respectively, which is resulted from the inflow of Tsugaru Warm Current (Takatsu et al., 2002). In the bay, cod larvae hatch from demersal eggs and migrate to pelagic waters by upward swimming and increasing buoyancy (Li et al., 2015). They are likely to experience variety in thermal experience owing to various hatching locations and dispersal along with the current[11] (Takatsu et al., 2002). Although they are considered to be opportunistic feeders in the bay (Takatsu et al., 2002), feeding cod larvae still probably suffer temporary food shortage, because of (1) uneven prey mass distribution in natural conditions (Letcher and Rice, 1997) and (2) departing from dense prey mass caused by the dispersal. Therefore, cod larvae confront potential risk of short-term mismatch in prey under thermal variations. However, very little is known about their behavioral responses to the two variables. Filling this knowledge gap will not only provide new information for future field sampling, but also improve the ability to forecast recruitment strength of this species in this bay.

The objective of this study was to test vertical distribution and swimming activity of Pacific cod larvae in relation to temporary prey shortage under varied temperatures. Cod larvae were tested at two stages after exogenous feeding. At either feeding stage,

[1] http://www.aomori-itc.or.jp/uminavi/hj_table.html

larvae received different prior feeding treatments: well fed (WF) or food deprivation (FD) for 24h. Upper-warm and bottom-warm temperature gradients were artificially generated in experimental vertical columns, ranging 4–8°C and 8–12°C, as well as a control condition (isotherm at 8°C). Vertical distributions and swimming activities were measured and compared in the five thermal patterns and at homogeneous temperatures (4, 8 and 12°C). These temperatures generally cover the lower and higher limits that are possibly experienced by Pacific cod larvae in Mutsu Bay. The results revealed ontogenetic changes in vertical distribution and in dominant factors affecting swimming activity,

2.2 Materials and Methods

2.2.1 Egg collection and larvae rearing

Adult Pacific cod were collected by bottom-set nets in Mutsu Bay, Japan during the spawning season in 2016 and 2017. Gametes from one female and three males were mixed and rinsed with seawater at about 4°C. Fertilized eggs were incubated in a hatching jar at 5.6±1°C. Six days later, a part of eggs were transported to the laboratory at Faculty of Fisheries, Hokkaido University in Hakodate within an insulated container. The eggs were incubated in a 5 L hatching jar at 6.2±0.1°C. After hatching, cod larvae were transferred into two low-through black fiberglass tanks (200 L) at a density of 15 larvae / L. Filtered seawater (33.8±0.3 in salinity) was supplied at a rate of 200 ml / min to either tank and maintained at 8.2±0.2°C. Overhead Light was provided with a fluorescent tube at a level of 3.8 μE m^{-2} s^{-1} at 12 h light : 12 h dark. Cod larvae were reared on enriched rotifers (*Brachionus plicatilis*) added at a density of 3–4 prey / ml

twice daily. An air stone was place at the bottom of either tank to ensure extra oxygen and homogeneous prey distribution. *Chlorella vulgaris* was added daily to either tank, to create green cultures for fish throughout the experimental period.

2.2.2 Vertical distribution of cod larvae

The experimental apparatus was based on that in Yoo et al. (2014) and consisted of three chambers, in each of which contained two cylindrical columns (diameter 10cm and height 85cm; Fig. 2.1). Each cylindrical column was filled to a depth of 75cm with artificial seawater (salinity 34; Tetra Marine Salt Pro, Spectrum Brands Japan Company), and divided into an upper section (depth 0–35cm) and a bottom section (depth 35–75cm). Seawater temperature in each section could be adjusted to 4°C, 8°C or 12°C by water bath. In this way, five thermal patterns were generated: pattern I, upper 40cm at 8–12 °C and bottom 35cm at 8°C; pattern II, upper 30cm at 8°C and bottom 45cm at 8–12 °C; pattern III, 8°C throughout the columns; pattern IV, upper 30 cm at 8°C and bottom 45cm at 4–8°C; pattern V, upper 40 cm at 4–8 °C and bottom 35cm at 8°C. Pattern II and V were generated by delicately injecting saline seawater (34) beneath less saline seawater (32) via a peristaltic pump (Fig. 2.1). Two fluorescent tubes were used to locate cod larvae in front of the columns, providing an approximately uniform light level of 2.5 $\mu E\ m^{-2}\ s^{-1}$. The uniform dim light was used to eliminate possible effects of light gradients on vertical distribution of Pacific cod larvae (Hurst et al., 2009) and accurately locate the fish larvae in the transparent vertical columns.

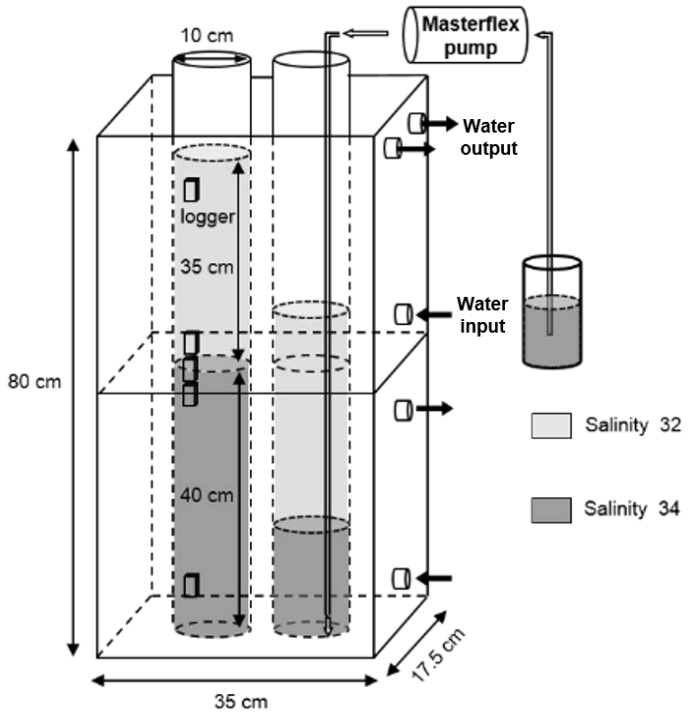

Fig. 2. 1 A diagram of plexiglass tank for vertical distribution of Pacific cod larvae. Two cylindrical vertical column were surrounded by an upper and a bottom sections acting as water bath with temperature-controlled circulations. Inversion thermal gradients were generated by slowly injecting salinity-34 seawater beneath salinity-32 seawater. Loggers were hang at 5, 30, 35, 40 and 70cm depths to record temperatures during the whole experimental period.

Some larvae were randomly captured from the two rearing tanks about 2h after the first feeding of the day and placed into polyethylene containers (400 ml) with air-bleed holes on the lids. They are maintained at 8°C in a temperature-controlled incubator without prey and half of the water was changed once during the next 24h. On the next experiment day, ten WF or FD larvae were introduced into each vertical column maintained at about 8°C, and temperature in each section was then adjusted to a target temperature (4, 8 or 12°C) in 4h. The larvae were acclimated to the vertical columns

and changing temperatures during this period. After the thermal pattern became stable, occurrences of larvae were recorded four times at 30-min intervals. Each recording including ten vertical positions of WF or FD larvae was treated as a replicate. These trials were repeated 4 times with young larvae at week 2 and twice with old larvae at week 4, due to limited number of available larvae, resulting in 16 replicates in the young larvae and 8 replicates in the old larvae.

2.2.3 Swimming activity of cod larvae

Swimming activity was classified into two behavioral categories: change in direction and change in position every minute, according to that of Colton and Hurst (2010; Table 2.1). Fifty WF or FD larvae were transferred into a horizontal cylindrical tank (14L, $n = 6$; Fig. 2.2) with seawater at 4.7±0.3, 8.6±0.2, or 12.2±0.2°C, and acclimated to the temperatures and/or tank for only 30 min, preventing temperature-induced ontogenetic difference. Side wall of each tank was covered by black polyester fiber to decrease reflection for the larvae and back side of each tank was covered by pale-green foam to improve visualization to locate the larvae. 25 of the 50 larvae were randomly selected after the acclimation, and swimming activity of individual larvae was recorded for 1 min with a video camera (HDR-CX 590, Sony, Tokyo). Repeated numbers of the trials were three time with the young larvae and twice with the old larvae.

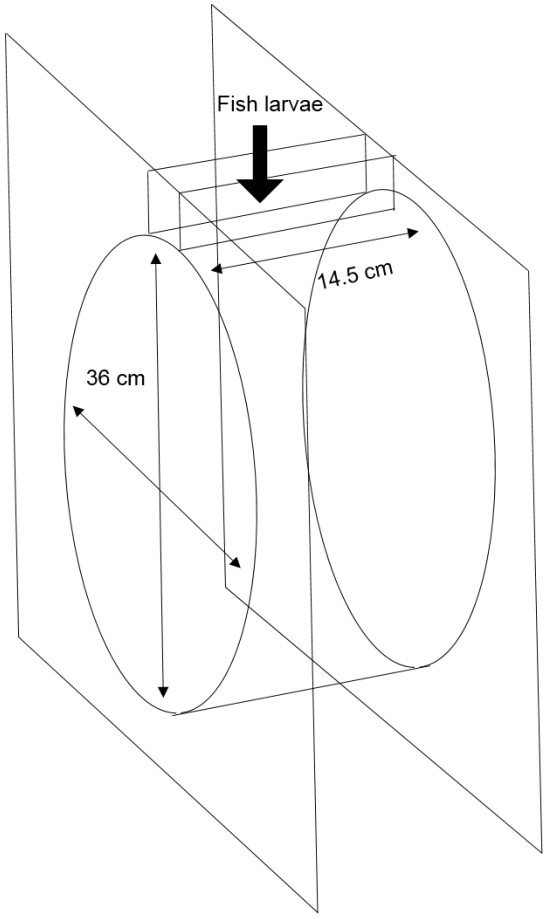

Fig. 2.2 A diagram of transparent horizontal cylindrical tank within which swimming activity of Pacific cod larvae were recorded. Each tank contained about 14 L seawater at 4, 8 or 12°C.

Table. 2.1 Descriptions of change in direction and change in position in cod larvae.

Category	Behavior	Description
Change in Direction	Rotate	Slow change in direction, using pelvic fins
	Turn	Rapid turn, using caudal fin
Change in position	Short swim	Move 0.5 to 3 body lengths, single tailbeat
	Long swim	Move 3 or more body lengths, multiple tailbeats

2.2.4 Data analysis

Individual larvae were either in the upper section or in the bottom section, according to their vertical position in a specific thermal pattern. Cochran–Mantel–Haenszel (C-M-H) Test was used to examine the difference in occurrences between WF and FD larvae in each thermal pattern at either stage. Wilcoxon signed-rank test was employed to compare numbers of cod larvae in the upper sections between the two stages. Data of change in direction and change in position every minute were combined together and treated as swimming activity. Differences in swimming activity were analyzed using two-way ANOVA with recent feeding conditions (N = 2) and temperature (N = 3) as main factors at either stage. Post-hoc tests were conducted using Tukey's HSD to identify the specific recent feeding condition where swimming activity varied with temperature and/or specific temperatures in which swimming activity differed between WF and FD larvae. Statistical significance was set at $p<0.05$.

Table. 2.2 Mean temperatures ± SD (°C) recorded by loggers at depths 5, 30, 35, 40 and 70 cm in the five thermal patterns.

Thermal pattern	Temperature ± SD (C) at depths (cm)				
	5	30	35	40	70
I	11.9 ± 0.3	11.8 ± 0.3	10.4 ± 0.5	8.5 ± 0.2	8.1 ± 0.2
II	8.2 ± 0.2	8.5 ± 0.2	9.6 ± 0.5	11.6 ± 0.2	11.7 ± 0.2
III	8.2 ± 0.2	8.3 ± 0.2	8.3 ± 0.1	8.2 ± 0.2	8.1 ± 0.1
IV	8.4 ± 0.2	8.2 ± 0.2	6.8 ± 0.5	4.7 ± 0.1	4.3 ± 0.1
V	4.5 ± 0.1	4.7 ± 0.1	5.8 ± 0.3	8.1 ± 0.2	8.2 ± 0.2

2.3 Results

2.3.1 Vertical distribution

All the thermal patterns were maintained steadily during the experiments

(Table 2.2). There were no differences in vertical distributions between WF and FD young larvae in pattern I, IV or V (Fig. 3 (a), (d) and (e)), and differences in occurrences of young larvae showed in pattern II (M-H-C test, $\chi^2 = 9.1$, $p = 0.002$; Fig. 2.3 (b)) and in pattern III ($\chi^2 = 11.5$, $p<0.001$; Fig. 2.3 (c)). Most young larvae occurred in the upper sections of the thermal patterns, regardless of temperature or recent feeding history (Fig. 2.3). A similar situation went on with the old larvae. There were no differences in occurrences between WF and FD old larvae in pattern I, II or V (Fig. 2.4 (a), (b) and (e)), and food-induced differences in occurrence was only shown in pattern III ($\chi^2 = 7.9$, $p = 0.005$; Fig. 2.4 (c)) and in pattern IV ($\chi^2 = 8.9$, $p = 0.003$; Fig. 2.4 (d)). However, old larvae were still more abundant in the upper sections of pattern III and pattern IV, except for FD old larvae in pattern III.

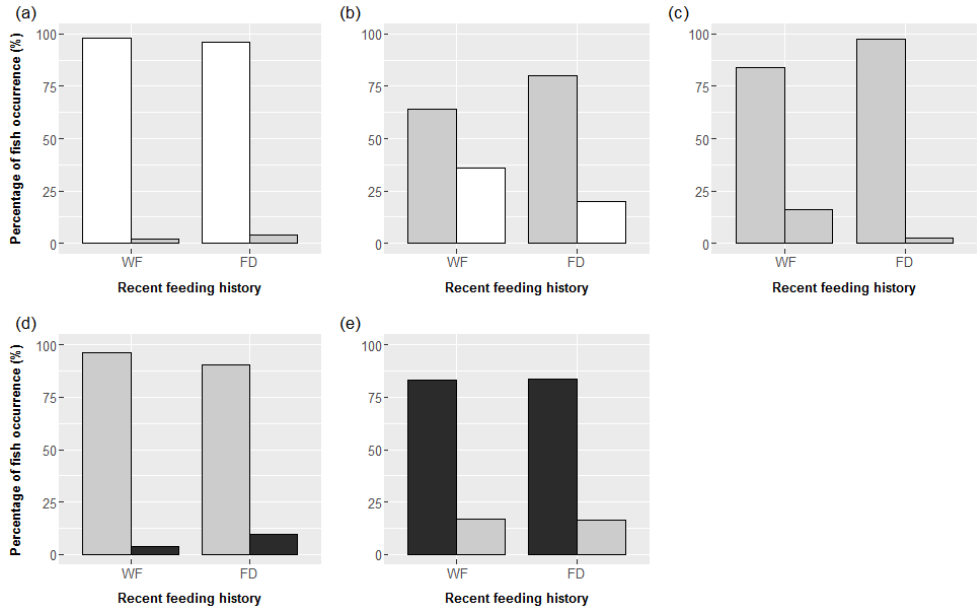

Fig. 2.3 Percentages of young larvae occurrences in the five thermal patterns with (a)–(e) corresponding to pattern I–V. In both WF and FD conditions, bars represent percentages of young larvae occurring in the upper (left) and bottom (right) sections in each thermal pattern. Colors of the bars represent depth-related temperatures with white for 8–12°C, grey for 8°C and black for 4–8°C.

Numbers of cod larvae in the upper sections decreased with age in all of the thermal pattern (Wilcoxon signed-rank test, $p<0.05$), with exceptions in WF larvae in pattern II ($p = 0.061$) and in FD larvae in pattern IV ($p = 0.055$), indicating that some old larvae descended into the bottom sections and some old larvae stayed in the upper sections (Fig. 2.4). Overall, recent feeding history did not affect vertical distributions of cod larvae throughout the thermal patterns in this study. Significant increase was found in the fraction of old larvae positioning themselves in the bottom sections when compared with young larvae.

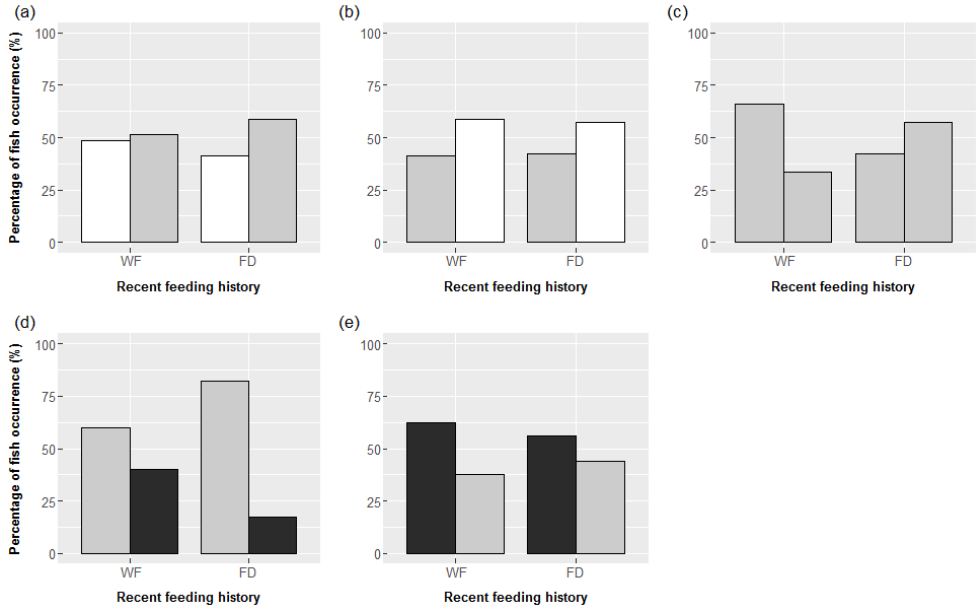

Fig. 2.4 Percentages of old larvae occurrences in the five thermal patterns with (a)–(e) corresponding to pattern I–V. In both WF and FD conditions, bars represent percentages of old larvae occurring in the upper (left) and bottom (right) sections in each thermal pattern. Colors of the bars represent depth-related temperatures with white for 8–12°C, grey for 8°C and black for 4–8°C.

2.3.2 Swimming activities

Within young larvae trials, temperature had a significantly positive effect on

swimming activity (two-way ANOVA, $p<0.001$; Fig. 2.5). WF larvae displayed an increase in swimming activity with temperature (Tukey's HSD test, $p<0.05$; Fig. 2.5), while FD larvae displayed a slight and non-significant increase in swimming activity. Recent feeding condition showed no effect on swimming activity in young larvae ($p = 0.18$; Fig. 2.5), and there was no significant difference in swimming activity between WF and FD young larvae in each temperature $p>0.05$; Fig. 2.5). As to old larvae, WF larvae exhibited higher swimming activities than FD larvae throughout the temperatures ($p<0.001$; Fig. 2.6), and swimming activities of both WF and FD old larvae were independent of temperature ($p = 0.29$; Fig. 2.6).

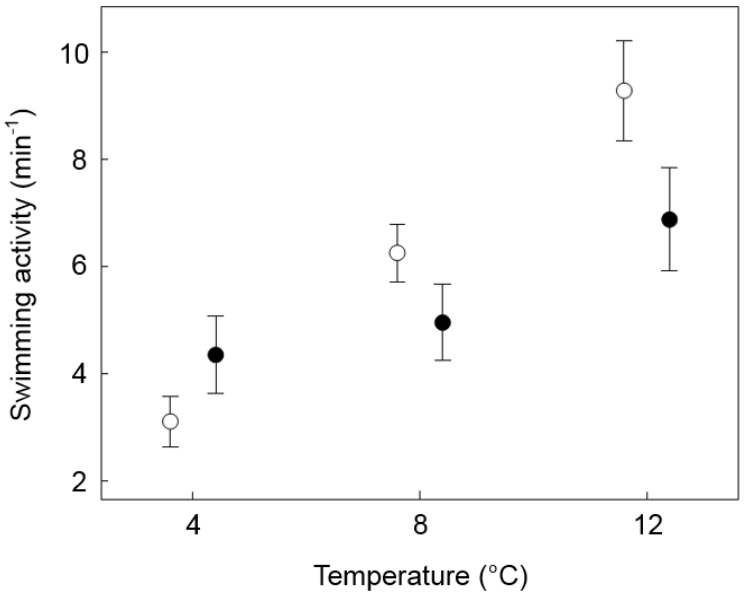

Fig. 2.5 Swimming activities of young WF and FD Pacific cod larvae at 4, 8 and 12°C. Open and filled symbols represent mean swimming activities of the WF and the FD larvae, respectively. Error bars represent ± SE.

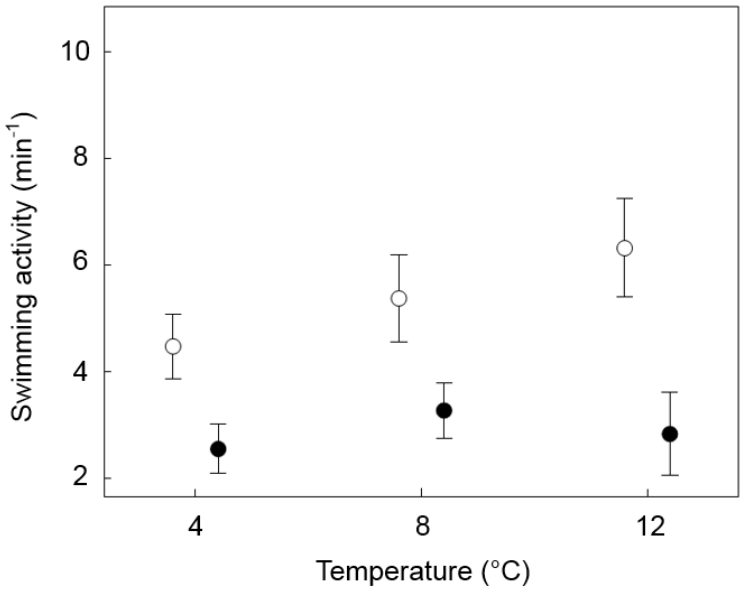

Fig. 2.6 Swimming activities of old WF and FD Pacific cod larvae at 4, 8 and 12°C. Open and filled symbols represent mean swimming activities of the WF and the FD larvae, respectively. Error bars represent ± SE.

2.4 Discussion

In this chapter, I examined vertical distribution and swimming activity of Pacific cod larvae in relation to temperature and recent feeding history. A short-term food deprivation for 24h did not affect vertical distribution of cod larvae throughout the temperature range which natural cod larvae would inhabit in, but this degree of food deprivation significantly reduced their swimming activities, especially in the old larvae. These behavioral responses to temperature and food conditions can be linked to vertical distributions and encounter rates with prey during the pelagic stages, which largely influences growth, survival and recruitment success.

Young cod larvae remained concentrated in the upper sections of the thermal patterns regardless of temperatures or recent feeding history. This upper distribution is consistent with the previous study by Hurst et al. (2009) reporting that smaller larvae of Pacific cod (6–10mm, SL) constantly stay in the upper sections of the vertical columns. In Mutsu Bay, it has been found that cod larvae (without yolk) were the most abundant at surface layers (15–20 m depths) in 1989, likely corresponding to the dense layer of their prey (Takatsu et al., 2002). Laboratory studies on other gadoid fish species have also indicated that walleye pollock *Gadus chalcogrammus* and Atlantic cod larvae are mainly distributed in the upper sections of temperature gradients at similar stages (Olla and Davis, 1990; Vollset et al., 2013). Thus, surface orientation is considered to be the dominant factor affecting vertical distribution at the earlier stage.

Surface orientation of fish larvae has been elucidated by a preference for warm temperature (e.g., Olla and Davis, 1990; Batty, 1994; Vollset et al., 2013) and prey

availability in Baltic cod larvae *Gadus morhua* in the Eastern Baltic Sea (Huwer et al., 2011). In the present study, inversion temperature gradients (bottom warmer) were generated and no food was supplied during the experimental period. However, young larvae did not dive into bottom-warm temperatures, but still maintained upper distribution. This suggests that neither warm-temperature preference nor access to prey might be the basic reason that leads to upper distribution in this species. Laboratory studies found that cod larvae actively swim upward very soon after hatching regardless of temperature (Forrester, 1964; Li et al., 2015) and smaller larvae (6–10 mm, SL) stay in upper depths over a wide range of light intensities (Hurst et al., 2009). Therefore, surface orientation of young cod larvae appears to be a result of intrinsic motivation. Similarly, some old larvae descended to bottoms sections may reflect an ontogenetic change in vertical habit. This phylogenetic development allows young larvae migrate upward into surface layers to start feeding, and old larvae to migrated downward to pursue larger prey (Huwer et al., 2011).

The increase in swimming activity of WF young larvae may reflect the temperature-dependent swimming ability (von Herbing, 2002). Starvation negatively impacts swimming ability in fish larvae (Laurence, 1972) and may consequently offset the promotion of swimming activity in the warm temperatures and contribute to a slight but non-significant increase in swimming activity in FD young larvae. Although the short-term food deprivation may restrain swimming activity, the similarity in swimming activity suggests that young larvae tend to increase swimming activity with temperature. This temperature-dependent swimming activity appeared to be determined

by physiology. Young larvae with smaller body sizes have limited swimming ability (Fisher et al., 2000) and low feeding success (von Herbing and Gallager, 2000). In warm temperatures, high swimming activity improves encounter with prey (Fouzai et al., 2015), and may compensate for the disadvantage of smaller larvae mentioned above and prevent high starvation mortality. Additionally, the young larvae may intend to grow rapidly and achieve a larger body size, which decreases stage-specific mortality, by increasing swimming activity to encounter and ingest more prey items especially at warm temperatures (Pepin, 1991). Saving energy by reducing swimming activity may not be an advantage for survival when mortality is high at the young stage (Vollset et al., 2013). Meanwhile, if young larvae experiencing short-term food shortage, this potential causes them to spend more energy on maintaining high swimming activity in warm temperatures. Hence, the young larvae are assumed to face elevated starvation risks.

The WF old larvae had significantly higher swimming activities than the FD old larvae across the temperatures, which is in line with the food-mediated swimming activity in Atlantic cod larvae at similar stages (Jordaan and Brown, 2003). This decrease in swimming activity of the FD larvae has been assumed to be a typical antipredator response and probably the only behavioral mechanism available to them for saving energy when they cannot achieve abundant prey items (Skiftesvik, 1992; Jordaan and Brown, 2003). In a starved state, fish larvae with decreased swimming ability are likely to be vulnerable to predators (Laurence, 1972; Yin and Blaxter, 1987). Only in this situation are starved fish larvae proposed to reduce swimming activity to

avoid predators. However, food deprivation even for 3 days does not affect escape ability of Atlantic cod larvae at 25 or 47 days after hatching at 10°C (Skajaa and Browman, 2007). Moreover. If prey are available, low energetic-state fish larvae still maintain substantial swimming activity to feed (Munk and Kiørboe, 1985; Puvanendran and Brown, 1999; Puvanendran et al., 2002), apparently ignoring accompanied predation risk (McNamara and Houston, 1987; Lienart et al., 2014). Therefore, the decreased swimming activity may not represent a behavioral response to reduce predation risk, but an energy-saving behavior. Instead of lower swimming activity, the constant swimming activity of the old larvae independent of temperature appears to be an antipredation reaction. As ontogeny, old larvae may experience a wider variety of temperatures in Mutsu Bay (Takatsu et al., 2002) and concentrate on water layers where high prey density and increased exposure to predators coexist (Garrison et al., 2000). Compared with young larvae, old larvae with larger body sizes may be more easily detected by visual predators (Litvak and Leggett, 1992). Therefore, old larvae dwelling in variable temperatures might select an optimal swimming activity to balance the trade-off between foraging activity and predation risk, independent of temperature.

Surface orientation and temperature-mediated swimming activity may promote growth and survival in young larvae in warm sea temperatures, meanwhile make FD individuals more vulnerable to starvation. It should be noted that exceptionally high fecundity of Pacific cod (Laurel et al., 2011) may make it possible to take such a “high-risk” strategy. Declined surface orientation combined with food-mediated swimming activity suggests that the old larvae have the capability of weighing the trade-off

between energetic state and swimming activity. During the stages, young larvae are suggested to migrate to deeper layers, and swimming activity was mediated by temperature in young cod larvae and by prior feeding in old cod larvae.

The study has highlighted the relevance of vertical behavior and swimming activity to growth potential under varying temperature and food conditions, using Pacific cod larvae, and revealed an ontogenetic change in growth strategy. This hypothesis can be tested by measuring mortality of cod larvae in the spatio-temporally variable thermal/prey field of Mutsu Bay. A field study with fine-scale sampling of cod larvae along with their prey and measurements of physical environment is encouraged.

Chapter 3

Vertical distribution and swimming activity of juvenile Pacific cod *Gadus macrocephalus* in relation to food availability and temperature

3.1 Introduction

In chapter 2, I tested the variations in vertical distribution and swimming activity of cod larvae under different thermal and food conditions, which to some extent verified the "match/mismatch hypothesis" from the perspective of behavioral response. This hypothesis is likely to be extended to the first summer of juvenile life since (*i*) age-0 fish may confront temporal-spatial food shortage due to distribution transition of prey organisms with season (Takatsu et al., 2001; Nakatani et al., 2003), and (*ii*) they must exceed a critical size or a minimum level of energy stores by the end of the first summer to improve winter survival (Beamish and Mahnken, 2001, Heintz et al., 2013). In addition, settled age-0 cod are believed to migrate out of Mutsu Bay in late June (Takatsu et al., 2001) and probably move northward to the waters adjacent to the Cape Esan, on the east side of the Tsugaru Strait (Kanno et al., 2001).

It has been widely accepted that no single factor is able to explain fish recruitment variability, but rather that multiple factors act together as determinants (Houde, 2008). In fish behavior research, numerous studies have linked temperature with food availability to investigate the interactive effect on juvenile fish behaviors (e.g., Sogard and Olla, 1996 and 1998; Nicieza and Metcalfe, 1997; Hurst and Duffy, 2005; Lienart

et al., 2014; Freitas et al., 2016) and indicated that juvenile fish often regulate vertical movement (thermoregulation behavior) and swimming activity based on individual energetic condition. For example, starved juvenile fish generally prefer cooler temperatures and decrease swimming activity in thermally stratified water to reduce energetic expenditure (Sogard and Olla, 1996; van Dijk et al., 2002; Killen, 2014). This kind of behaviors has been explained in the light of growth trajectory involving physiological processes, namely a trade-off of energetic allocation between (compensatory) growth and metabolism costs (Killen, 2014). Swimming activity varies with not only temperature (Sogard and Olla, 1998; Hurst, 2007) but also recent feeding history (van Dijk et al., 2002). Model studies regard swimming activity of larval fish as a function of temperature and food availability (Jørgensen et al., 2014; Fouzai et al., 2015), suggesting that that larval fish must weigh feeding opportunity and predation risk, and finally take an optimal swimming activity in a specific temperature-food condition. It seems that changes in vertical distribution and swimming activity involve varying temperature and food availability.

Pacific cod (hereafter cod) *Gadus macrocephalus* is a commercially and ecologically important marine fish species (Laurel et al., 2007) and widely distributed along the continental shelve of the North Pacific Ocean (Alderdice and Forrester, 1971). Newly hatched larvae migrate to surface waters very soon (Hurst et al., 2009) via upward swimming and increasing buoyancy (Li et al., 2015). The upper limit of habitat temperature of age-0 cod is considered to be 12°C in the Northern Japan (Takatsu et al., 2001; Morioka and Kuwada, 2002). In laboratory, age-0 cod adjust vertical positions

with light levels and avoid cold waters as low as 3°C (Davis and Ottmar, 2009). This area on the east side of the Tsugaru Strait is the confluence of the Tsugaru Warm Current and the cold Oyashio Current, and thus juvenile cod in this area also experience remarkable changes in thermal conditions, accompanied with low food availability due to thermal extremes (Sakurai, 2007). Understanding their behavioral response of age-0 cod to the environmental variables is of great significance for predicting their growth and survival, as well as providing implications for recruitment and stock productivity (Kristiansen et al., 2014). However, limited study has focused on swimming behaviors of age-0 cod under such complicated natural conditions.

The objective of this study was to test the effects of temperature and recent feeding history on vertical distribution and swimming activity of age-0 cod. Age-0 cod either fed *ad libitum* (well fed, WF) or food-deprived (FD) for 24h were tested in experimental conditions including temperature gradients and homogenous temperatures, including warm scenarios (range 8–12°C) and cold scenarios (range 4– 8°C). The results of swimming behaviors are discussed with regards to the effects on growth and survival, helping us to understand the recruitment of this species at the vital stage especially in the area of southern Hokkaido.

3.2 Materials and methods

3.2.1. Fish rearing

Age-0 cod were collected using bottom set-nets offshore the Furube, southern Hokkaido, Japan (Fig. 1.1) in late May 2015 and 2016. Fish were transported within

insulated containers to the laboratory at Faculty of Fisheries Sciences, Hokkaido University in Hakodate, Japan. The fish were acclimated at 8–9°C for one week in a black conical tank (1000 L) at 12 : 12 h light : dark with a daytime light level of 1 to 14.3 μE m^{-2} s^{-1} at the water surface. The juveniles were fed with thawed krill to satiation twice daily.

3.2.2 Vertical distribution of age-0 cod

The experimental apparatus was the same as Fig. 2.1 in Chapter 2. The pattern I, III and IV generally occur in all ocean conditions, while pattern V may occur in the Oyashio region (Sakurai, 2007). Although it seldom occurs in ocean conditions, pattern II was generated to create temperature rising from blow. A red-filtered light ($<4\times10^{-2}$ μE m^{-2} s^{-1}) hang above the columns was used to locate juvenile cod under a dark condition to eliminate effects of light level on vertical movement of the age-0 cod (Davis and Ottmar, 2009).

Some juveniles were separated and deprived of food 24h prior to each trial (n = 10). Three WF or FD cod with a similar body size (57.9 ± 6.9mm, mean ± SD in SL) were captured from the rearing tank and transferred into each vertical column maintained at about 8°C. Temperature in each section was changed to a target temperature (4, 8 or 12°C) and each thermal pattern became stable 4h later. After that, depths of cod were recorded for 4 times at 30-min intervals in each thermal pattern. Each recording including three fish depths was used for a replicate (n = 40).

3.2.3 Swimming activity of age-0 cod

The experiment of swimming behavior was conducted in a plexiglass horizontal column tank (67cm diameter, 30cm width, 100 L) imbedded within a concrete case used for water bath, in which a cooler and a heater were used to control temperature. The front side of the concrete case was a plexiglass window uncovered for video recording during the experiment, while the back and top side were covered to reduce reflection to the cod. Swimming activity included two categories: change in direction and change in position per unit time (See Table 2.1 in Chapter 2). Activity level stands for the ability of fish to locate and remain within micro-patches of high prey abundance (Jenkins,1988; Letcher and Rice, 1997; Colton and Hurst, 2010) and reflects predation risk (Fiksen and Jørgensen, 2011), involving functions of antipredator and energy saving (Skiftesvik,1992; Jordaan and Brown, 2003).

Ten WF or FD cod were introduced into the tank maintained at about 8°C. They were allowed to acclimated to the tank, as well as the ambient temperature which would be chilled to 4°C (4.7±0.3°C), maintained at 8°C (8.7±0.2°C) or raised to 12°C (12.3±0.2°C) overnight. In the next morning, swimming activities of 10 cod were recorded with a video camera suitably positioned to cover all the fish in the tank for 2 min. Three replicates were conducted in each combination of temperature and recent feeding history.

3.2.4 Data analysis

Vertical distribution was divided into either upper or bottom distribution, according

to individual depth in a specific thermal pattern. Difference in vertical distribution between WF and FD juveniles was examined using Cochran–Mantel–Haenszel (C-M-H) Test with individual numbers in upper and bottom section in each thermal pattern. Two–way ANOVA was used to examine the effects of temperature and recent feeding condition on frequencies of direction change and position change. Tukey's HSD post-hoc tests were employed to analyze specific temperatures in which swimming activity differed between WF and FD cod and/or specific recent feeding condition in which swimming activity varied among temperatures when statistical difference was determined in either variable. Statistical significance was set at $p<0.05$.

Table. 3.1 Mean temperatures ± SD (°C) recorded by loggers at depths 5, 30, 35, 40 and 70 cm in the cylindrical tanks.

Thermal pattern	Temperature ± SD (°C) at various depths (cm)				
	5	30	35	40	70
I	12.4 ± 0.1	12.0 ± 0.2	10.7 ± 0.3	8.4 ± 0.2	8.1 ± 0.1
II	8.1 ± 0.1	8.7 ± 0.9	10.3 ± 0.7	11.8 ± 0.5	11.9 ± 0.4
III	8.2 ± 0.1	8.0 ± 0.1	8.0 ± 0.1	8.0 ± 0.1	8.0 ± 0.1
IV	8.3 ± 0.5	8.1 ± 0.5	6.8 ± 0.3	4.8 ± 0.1	4.6 ± 0.1
V	4.6 ± 0.1	4.7 ± 0.2	6.1 ± 0.5	8.0 ± 0.5	8.3 ± 0.5

3.3 Results

Depth-specific temperatures in each thermal pattern were illustrated in Table 3.1. The juveniles exhibited various vertical distributions depending on thermal pattern and recent feeding history. In pattern I, WF juveniles were more abundant than FD juveniles in the upper section at 8–12°C (C-M-H test, $\chi^2 = 15.74$, $p<0.001$; Fig. 3.1(a) and Fig. 3.2(a)), indicating that the former did not avoid the warm temperature of 12°C, but the

latter did. Although difference in vertical distributions was determined between WF and FD juveniles in pattern II ($\chi^2 = 8.50$, $p = 0.004$; Fig. 3.1(b) and Fig. 3.2(b)), most of them occurred in the bottom section at 8–12°C. In pattern III, no difference in vertical distribution showed between WF and FD juveniles ($\chi^2 = 2.14$, $p = 0.14$; Fig. 3.1(c) and Fig. 3.2(c)). In pattern IV, WF juveniles were more abundant in the bottom section at 4–8°C than FD juveniles ($\chi^2 = 22.46$, $p < 0.001$; Fig. 3.1(d) and Fig. 3.2(d)), indicating that the former did not avoid the cold temperature of 4°C, but the latter did. Similar to those in pattern II, WF and FD juveniles mostly stayed in the bottom section at 8°C in pattern V ($\chi^2 = 2.36$, $p = 0.12$; Fig. 3.1(e) and Fig. 3.2(e)). Overall, WF cod occurred a broader range of temperatures (4–12°C), while FD cod tended to stay in the acclimated temperature (8°C), except that in pattern II and V.

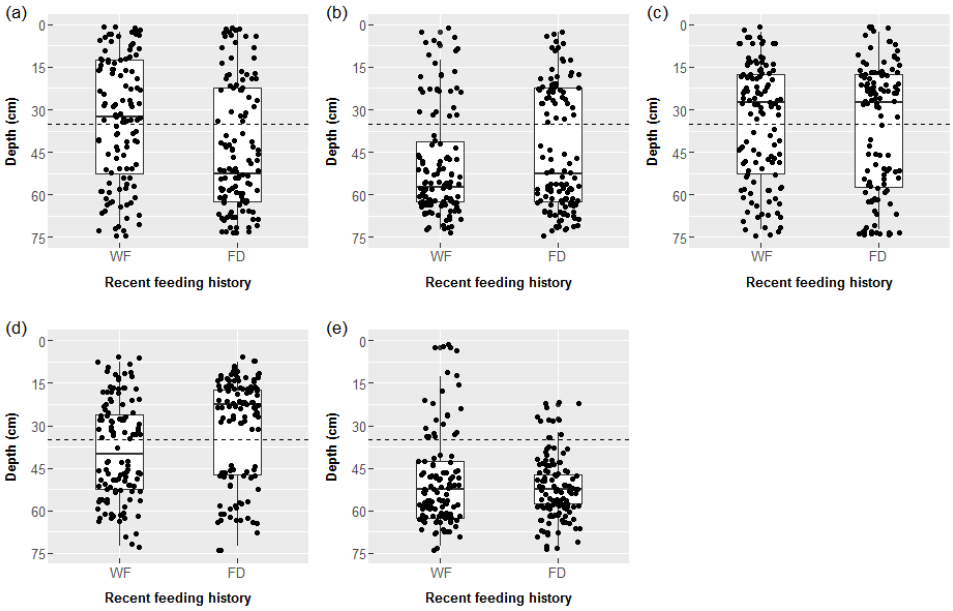

Fig. 3.1 Depths of age-0 juvenile Pacific cod in the five thermal patterns with (a)–(e) corresponding to pattern I–V. Boxes with error bars represent the lowest, 25 percentile, median, 75 percentile and the highest depths. Black points represent occurrences of age-0 juvenile Pacific cod.

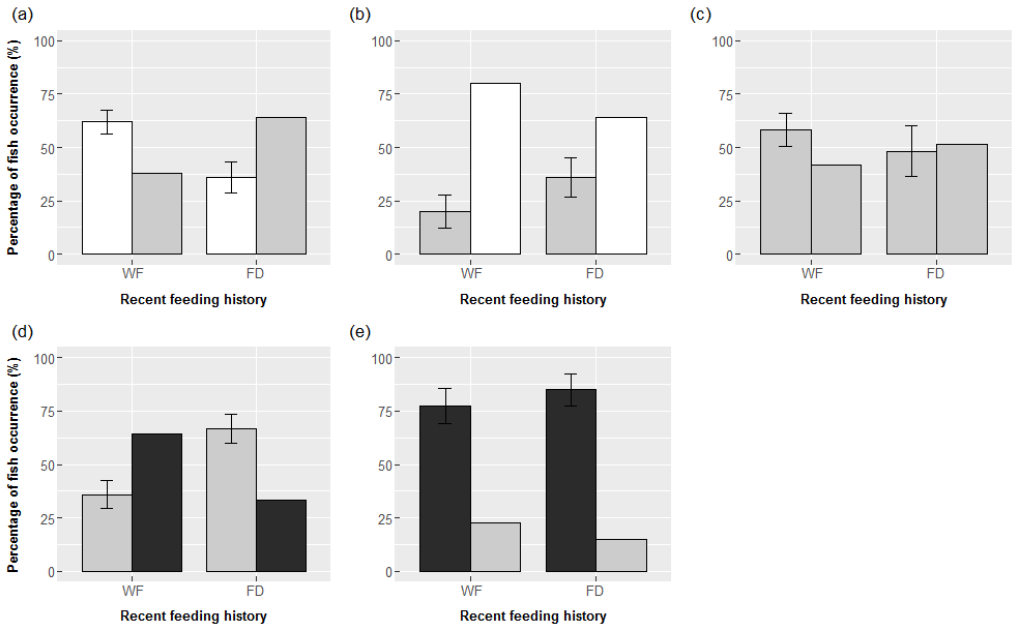

Fig. 3.2 Percentages of age-0 cod occurrences in the five thermal patterns with (a)–(e) corresponding to pattern I–V. In both WF and FD conditions, bars represent percentages of juveniles occurring in the upper (left) and bottom (right) sections in each thermal pattern. Colors of the bars represent depth-related temperatures with white for 8–12°C, grey for 8°C and black for 4–8°C. Error bars represent ± SD.

Temperature significantly affected the both categories of swimming activity in the juveniles (Two-way ANOVA, p <0.001). In the trials with WF individuals, swimming activity was the highest at 12°C (Tukey's HSD test, $p < 0.05$; Fig. 3.3(a) and (b)) and no difference in swimming activity showed between 4 and 8°C ($p > 0.05$; Fig. 3.3(a) and (b)). In the trials with FD juveniles, swimming activity was the lowest at 4°C ($p <$ 0.05; Fig. 3.3(a) and (b)) but no difference in swimming activity showed between 8 and 12°C ($p > 0.05$; Fig. 3.3(a) and (b)). In each temperature, there was no difference in swimming activity between WF and FD cod in either category, except that WF cod exhibited more frequent change in direction than FD cod at 8°C ($p < 0.05$; Fig. 3.3(a) and (b)). Overall, the WF cod maintained lower swimming activity at 4–8°C and

attained the highest swimming activity at 12°C, while the FD cod achieved the lowest swimming activity at 4°C and maintained higher swimming activities at 8 and 12°C.

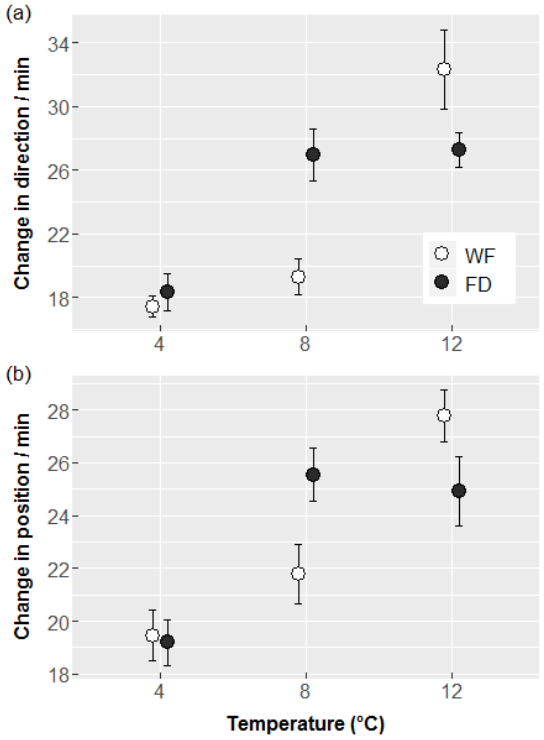

Fig. 3.3 Frequencies of change in direction and change in position of age-0 Pacific cod at 4, 8 and 12°C. Open and filled symbols represent mean swimming activities of the WF and the FD larvae, respectively. Error bars represent ± SE.

3.4 Discussion

The present study explored effects of short-term food shortage on vertical distribution and swimming activity of age-0 juveniles of Pacific cod in various temperature conditions. The results showed that the FD juveniles concentrated in the acclimated temperature, and exhibited different changes in swimming activity with temperature, compared to WF juveniles. Habitat selection is an integrated decision made by aquatic individuals, involving trade-offs between multiple requirements and

constraints in natural conditions (Sih, 1980; Werner et al., 1983; Orians and Wittenberger, 1991), such as the trade-off between temperature and food availability impacting habitat selection in cold-water marine fish (Freitas et al., 2016). Environmental variability in temperature and food availability interacting in the bioenergetics of aquatic ectotherms affect physiological condition, growth rate, survival and behavior (Wildhaber and Crowder,1990; Nicieza and Metcalfe, 1997; McLeod et al., 2013; Fouzai et al., 2015;). For example, juvenile fish that exposed to food deprivation improve growth efficiency by residing in cooler waters (Killen, 2014).

Previous studies with juvenile walleye pollock and cod have indicated that the juvenile gadids avoided cold temperatures as low as 2–3°C (Sogard and Olla, 1996; Davis and Ottmar, 2009). In the present study, the cold temperature of 4°C might not be low enough to trigger avoidance in WF juvenile cod. Meanwhile, this temperature may increase energy reserve (lipid) in the age-0 juvenile cod (Sreenivasan and Heintz, 2016). A field study over warm and cold climates has also documented that on age-0 juvenile cod are smallest but have highest energetic states in cold sea temperatures (Farley et al., 2016). On the other hand, the cold temperature did result in avoidance in FD juvenile cod, and largely reduced swimming activity of FD juveniles. The avoidance of the cold temperature and the sharp decrease in swimming activity suggest that age-0 juvenile cod may be more sensitive to the decrease in temperature from 8 to 4°C when deprived of food for 24h.

Prior to the present study, it had been unknown that how age-0 juvenile cod behaviorally response to increased temperature in vertical columns. Unlike FD

juveniles, WF juveniles did not avoid the warm temperature of 12°C. In late spring and early summer, the upper limit of temperature of the species is thought to be 12°C in the northern Japan (Takatsu et al., 2001; Morioka and Kuwada, 2002). Whether habiting in a temperature as warm as 12°C appears to depend on prey availability to survival benefit of juvenile cod at this stage. Hurst et al. (2010) measured growth rate of juvenile cod ranging 2–11°C at a similar body size and argued that growth rate increased with temperature until 12°C when prey supply is sufficient. The high swimming activity at 12°C may improves feeding rate (Fouzai et al., 2015), which is be able to satisfy metabolic demands and ensure the possible promotion of warm temperature on growth rate. In this case, age-0 juvenile cod may keep a substantially high growth rate until the autumn and attain a larger body size which is an advantage to them to go through the first winter (Beamish and Mahnken, 2001).

FD juveniles avoided the warm and the cold temperatures and tended to stay in the acclimated temperature. These vertical behaviors indicate that as ectothermic animal, the juveniles can select temperature-specific microhabitats based on individual energetic conditions. Furthermore, the food-induced thermoregulation behaviors are generally consistent with those of juvenile walleye pollock *Gadus chalcogrammus*: starved individuals utilize lower temperatures as energy-conserving refuges in the gradual temperature gradients, and decrease movements into cold waters in sharp temperature gradients (Sogard and Olla, 1996). However, this pattern of thermoregulation varies with species. For example, age-0 brown trout *Salmo trutta* always preferred a lower temperature when well fed, which is explained with regard to

optimal temperatures for growth rate (Elliott and Allonby, 2013). Moreover, the assemblages of WF and FD juveniles in pattern II and V might be that they are restricted to the bottom section by cold waters occurring above under darkness. Age-0 juvenile cod, like age-0 juvenile walleye pollock around the same area, may carry out diel vertical migration, distributed in upper-warm waters at night (Davis and Ottmar, 2009; Kawauchi et al., 2014). However, the temperatures were lower in the upper sections, and they avoid cold waters (Davis and Ottmar, 2009). Therefore, they concentrated in the bottom sections under the darkness, regardless of temperatures there. The thermal pattern II and V may rarely occur in the Oyashio region characterized by low temperature and low salinity (Sakurai, 2007) and deep mixed layer during winter and early spring (Ikeda et al., 2008). When this thermal patterns appear, age-0 juvenile cod are expected to be restrained in deeper water layers at night.

The present study examining the swimming behaviors of age-0 juvenile cod in relation to temperature and recent feeding history, indicating that vertical distribution of age-0 juvenile cod was associated with recent feeding history in temperature gradients and that they were capable of regulating energetic expenditure based on individual energetic state by swimming activity at this vulnerable and vital stage (Heintz and Vollenweider, 2010). In the confluence region of the Tsugaru Warm Current and the Oyshio Current in the southern Hokkaido, age-0 cod are possibly subjected to temporary food shortage in warm and cold extremes (Sakurai, 2007). Starved cod are expected to avoid warm and cold waters and to be distributed in moderate temperatures. When prey is available in cold waters, they are supposed to

adapt gradually to the cold temperatures and ingest prey (Davis and Ottmar, 2009). When food is available in warm waters, starved cod are also expected to move into the warm temperatures to feed. Thus, the selection of their thermal environment depends on the balance between benefit from feeding and metabolic costs. If the higher temperature is not lethal and the benefit from feeding exceeds metabolic costs, starved cod might move into warm waters to feed and return to cool waters (Sims et al., 2006).

During the experiments, food was not introduced to the cod because the limited space of experimental devices. Studies conducted in broader spaces indicate that feeding contributes to increases in swimming activity in both thermally homogeneous and stratified waters (Moberg et al., 2011; Davis and Ottmar., 2009). Moreover, predation plays another major role in determining juvenile survival (Houde, 1987) and not considered in this study. Further studies on feeding opportunity and predation risk are therefore strongly recommended to explore the interactive effects of temperature gradients and food availability on the trade-off between foraging activity and predation risk assessment.

Chapter 4

General discussion

The objective of this dissertation was to examine the effects of varying temperatures and prey availability on swimming behaviors of larval and juvenile (age-0) Pacific cod. The cod larvae were artificially hatched from eggs in Mutsu Bay and the juvenile cod were captured from the areas on the east side of the Tsugaru Strait in Southern Hokkaido. Both the areas are characterized by temperature dynamics to the fish. Vertical thermal structures were manipulated and combined with prior feeding conditions to test vertical distribution and swimming activity of the fish under experimental conditions.

The results revealed obvious differences in swimming behaviors between larval and juvenile cod. The range of tolerable temperature of larval fish is more narrow than that of juvenile fish **(**Pörtner and Farrell, 2008). In this study, however, cod larvae hardly exhibited response to the temperature settings compared to age-0 juvenile cod, and only regulated swimming activity based on temperature or recent feeding history (**Chapter 2**). On the other hand, age-0 juvenile cod adjusted not only vertical behaviors in temperature gradients but also swimming activity when restrained in homogenous temperatures (**Chapter 3**).

Combining the present results with those of Li et al. (2015), cod larvae migrate upward soon after hatching, stay in surface waters and are speculated to gradually

migrate oppositely to deeper waters. These results suggest that earlier cod larvae (yolk-sac larvae and the young larvae) exhibit negative geotaxis, and that later larvae (the old in the present study) commence to exhibit positive geotaxis. A similar migration pattern occurs to Baltic cod larvae and has been explained by ontogenetic changes in requirements for prey availability, as well as temperature (Grønkjær and Wieland, 1997; Huwer et al., 2011). This experimental study indicate that the migration pattern might also be controlled by phylogeny. During earlier larval stages, surface orientation (negative geotaxis) might be the dominance affecting vertical distribution. In other words, cod larvae may be fixed in surface water layers no matter what temperature is there or what their recent feeding is (Discussion in Chapter 2). Hatching areas of cod larvae in Mutsu Bay may be widespread and vary with years (the bay mouth and the inner bay; Takatsu et al., 2002). Cod larvae may migrate upward to and then stay in surface waters with various temperatures (Bian et al., 2014; Li et al., 2015). This does not mean that a variety of temperatures are suitable to cod larvae, considering prey availability. Instead, negative geotaxis may force cod larvae to stay in surface waters and they have to passively experience a wider range of temperatures.

Cod Larvae did not select preferred temperatures vertically in this study, but they did exhibit changes in swimming activity based on recent feeding condition. Meanwhile, age-0 cod regulated not only temperature experienced but also swimming activity, based on recent feeding history (Results in Chapter 2 and Chapter 3). These behavioral differences may imply different ways of energetic expenditure between larval and juvenile cod experiencing different recent feeding conditions. Behavioral mechanism

of Pacific cod appears to be more complicated with their physiological development. Thus, the age-0 cod are expected to be stronger and much more flexible than the cod larvae in coping with various thermal and prey conditions, and the old larvae are more resistible than the young larvae.

The clade ancestor of Pacific cod is thought to originate from Arctic and speciation of this species is determined by recurrent adaption to moderate thermal conditions. Compared to other gadid species, this species is distributed more southward in Asian marine waters, (Owens, 2015). In addition, the influence of the Tsugaru Warm Current can not be neglectable. The subpopulation of Pacific cod in this area must have stronger ability to adapt to relative warm conditions and survival to now. When involving prey availability, however, it become difficult to forecast effects of the environmental variables on fish recruitment. The interaction of temperature and prey availability on fish is complicated and there is still much work to be done.

In this dissertation, only temperature and recent feeding history were treated as main environmental factors. Both field and laboratories studies have revealed that light intensity affects vertical movements of larval and juvenile Pacific cod (Hurst et al., 2009; Davis and Ottmar, 2009). Further, light may play a more important role in larval vertical movement than temperature (Olla and Davis, 1990). Thus, light intensity as another environmental factor is strongly recommended to be introduced into future studies.

Feeding behaviors of larval and juvenile cod are often studied in small tanks which may be stressful to larval fish (Houde, 2008). The tanks used in chapter 2 and chapter

3 were also considered too small to clarify feeding behavior of the fish, so only swimming activities were tested. Further studies must evaluate the stress of experimental systems on objectives (larval and juvenile fish) and find out suitable and available equipment to test feeding behaviors. To discuss about feeding behaviors *in situ*, there is still a large gap of knowledge.

Numerous studies have related swimming behaviors of fish to their growth, survival and even recruitment success. In natural conditions, field surveys have only revealed vertical movements in response to varying temperature, light and prey. Furthermore, the question that to what extent this sort of individual-scale swimming behaviors affect fish growth, survival and influence recruitment seems to be too difficult to answer. Thereby, how to weigh the role played by the individual-scale swimming behaviors in the vital indicators is very urgent in future fishery oceanography.

References

Alderdice, D., Forrester, C., 1971. Effects of salinity, temperature, and dissolved oxygen on early development of the Pacific cod (*Gadus macrocephalus*). J. Fish. Res. Board. Can. 28, 883-902.

Andrade, C. A., Brazão, I. P., Nogueira, N., Ferreira, M. P., Dillinger, T., Dinis, M. T., Narciso, L., 2011. Red porgy (*Pagrus pagrus*) larval feeding performance and behavior at the onset of exogenous feeding. J. Exp. Mar. Biol. Ecol. 407, 377-381.

Bailey, K. M., 2000. Shifting control of recruitment of walleye pollock *Theragra chalcogramma* after a major climatic and ecosystem change. Mar. Ecol. Prog. Ser. 198, 215-224.

Bailey, K. M., Ciannelli, L., Bond, N. A., Belgrano, A., Stenseth, N. C., 2005. Recruitment of walleye pollock in a physically and biologically complex ecosystem: a new perspective. Prog. Oceanogr. 67, 24-42.

Bakkala, R., Westrheim, S., Mishima, S., Zhang, C., Brown, E., 1984. Distribution of Pacific cod *(Gadus macrocephalus*) in the north Pacific Ocean. Int. Nor. Pac. Fish. Comm. Bull. 42, 111-115.

Batty, R., 1994. The effect of temperature on the vertical distribution of larval herring (*Clupea harengus* L.). J. Exp. Mar. Biol. Ecol. 177, 269-276.

Beamish, R. J., Mahnken, C., 2001. A critical size and period hypothesis to explain natural regulation of salmon abundance and the linkage to climate and climate change. Prog. Oceanogr. 49, 423-437.

Beaugrand, G., Brander, K. M., Souissi, J. A. L. S., Reid, P. C., 2003. Plankton effect

on cod recruitment in the North Sea. Nature 426, 661.

Bian, X., Zhang, X., Sakurai, Y., Jin, X., Gao, T., Wan, R., Yamamoto, J., 2014. Temperature-mediated survival, development and hatching variation of Pacific cod *Gadus macrocephalus* eggs. J. Fish Biol. 84, 85-105.

Bochdansky, A., Grønkjær, P., Herra, T., Leggett, W., 2005. Experimental evidence for selection against fish larvae with high metabolic rates in a food limited environment. Mar. Biol. 147, 1413-1417.

Boehlert, G. W., Gadomaski, D., Mundy, B., 1985. Vertical distribution of ichthyoplankton off the Oregon coast in spring and summer months. Fish. Bull. 83, 611-622.

Breau, C., Cunjak, R. A., Peake, S. J., 2011. Behaviour during elevated water temperatures: can physiology explain movement of juvenile Atlantic salmon to cool water? J. Anim. Ecol. 80, 844-853.

Bryan, J., Kelsch, S., Neill, W., 1990. The maximum power principle in behavioral thermoregulation by fishes. T. Am. Fish. Soc. 119, 611-621.

Busby, M., Duffy-Anderson, J., Mier, K., Forest, L., 2014. Spatial and temporal patterns in summer ichthyoplankton assemblages on the eastern Bering Sea shelf 1996–2007. Fish. Oceanogr. 23, 270-287.

Catalán, I. A., Vollset, K., Morales-Nin, B., Folkvord, A., 2011. The effect of temperature gradients and stomach fullness on the vertical distribution of larval herring in experimental columns. J. Exp. Mar. Biol. Ecol. 404, 26-32.

Clark, D. L., Leis, J. M., Hay, A. C., Trnski, T., 2005. Swimming ontogeny of larvae

of four temperate marine fishes. Mar. Ecol. Prog. Ser. 292, 287-300.

Colton, A. R., Hurst, T. P., 2010. Behavioral responses to light gradients, olfactory cues, and prey in larvae of two North Pacific gadids (*Gadus macrocephalus* and *Theragra chalcogramma*). Environ. Biol. Fish. 88, 39-49.

Coyle, K., Eisner, L., Mueter, F., Pinchuk, A., Janout, M., Cieciel, K., Farley, E., Andrews, A., 2011. Climate change in the southeastern Bering Sea: impacts on pollock stocks and implications for the oscillating control hypothesis. Fish. Oceanogr. 20, 139-156.

Cushing, D., 1990. Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. Adv. Mar. Biol. 26, 249-293.

Davis, M. W., Ottmar, M. L., 2009. Vertical distribution of juvenile Pacific cod *Gadus macrocephalus*: potential role of light, temperature, food, and age. Aquat Biol 8, 29-37.

Ellertsen, B., Solemdal, P., Strømme, T., Tilseth, S., Westgård, T., Moksness, E., Øiestad, V., 1980. Some biological aspects of cod larvae (*Gadus morhua* L.). Fiskeridir. Skr., Ser. Havunders. 17, 29 – 47.

Elliott, J. M., Allonby, J. D., 2013. An experimental study of ontogenetic and seasonal changes in the temperature preferences of unfed and fed brown trout, *Salmo trutta*. Freshw. Biol. 58, 1840-1848.

Farley, E. V., Heintz, R. A., Andrews, A. G., Hurst, T. P., 2016. Size, diet, and condition of age-0 Pacific cod (*Gadus macrocephalus*) during warm and cool climate states in the eastern Bering Sea. Deep-sea Res. Part II. 134, 247-254.

Fiksen, Ø., Jørgensen, C., 2011. Model of optimal behaviour in fish larvae predicts that food availability determines survival, but not growth. Mar. Ecol. Prog. Ser. 432, 207-219.

Fiksen, Ø., Jørgensen, C., Kristiansen, T., Vikebø, F., Huse, G., 2007. Linking behavioural ecology and oceanography: larval behaviour determines growth, mortality and dispersal. Mar. Ecol. Prog. Ser. 347, 195-205.

Fisher, R., Bellwood, D. R., Job, S., 2000. Development of swimming abilities in reef fish larvae. Mar. Ecol. Prog. Ser. 202, 163-173.

Folkvord, A., 2005. Comparison of size-at-age of larval Atlantic cod (*Gadus morhua*) from different populations based on size-and temperature-dependent growth models. Can. J. Fish. Aquat. Sci. 62, 1037-1052.

Forrester, C., 1964. Laboratory observations on embryonic development and larvae of the Pacific cod (*Gadus macrocephalus* Tilesius). J. Fish. Res. Board. Can. 21, 9-16.

Fouzai, N., Opdal, A. F., Jørgensen, C., Fiksen, Ø., 2015. Effects of temperature and food availability on larval cod survival: a model for behaviour in vertical gradients. Mar. Ecol. Prog. Ser. 529, 199-212.

Freitas, C., Olsen, E. M., Knutsen, H., Albretsen, J., Moland, E., 2016. Temperature-associated habitat selection in a cold-water marine fish. J. Anim. Ecol. 85, 611-613.

Garrison, L. P., Michaels, W., Link, J. S., Fogarty, M. J., 2000. Predation risk on larval gadids by pelagic fish in the Georges Bank ecosystem. I. Spatial overlap associated with hydrographic features. Can. J. Fish. Aquat. Sci. 57, 2455-2469.

Georgalas, V., Malavasi, S., Franzoi, P., Torricelli, P., 2007. Swimming activity and

feeding behaviour of larval European sea bass (*Dicentrarchus labrax* L): effects of ontogeny and increasing food density. Aquaculture 264, 418-427.

Grønkjær, P., Wieland, K., 1997. Ontogenetic and environmental effects on vertical distribution of cod larvae in the Bornholm Basin, Baltic Sea. Mar. Ecol. Prog. Ser. 154, 91-105.

Heintz, R. A., Vollenweider, J. J., 2010. Influence of size on the sources of energy consumed by overwintering walleye pollock (*Theragra chalcogramma*). J. Exp. Mar. Biol. Ecol. 393, 43-50.

Heintz, R. A., Siddon, E. C., Farley, E. V., Napp, J. M., 2013. Correlation between recruitment and fall condition of age-0 pollock (*Theragra chalcogramma*) from the eastern Bering Sea under varying climate conditions. Deep-sea Res. Part II. 94, 150-156.

Hjort, J. 1914. Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. Rapp. Conserv. Explor. Mer. 20:1-228.

Houde, E., Hoyt, R., 1987. Fish early life dynamics and recruitment variability, Am. Fish. Soc. Symp., 2, 17–29.

Houde, E. D., 1989. Comparative growth, mortality, and energetics of marine fish larvae: temperature and implied latitudinal effects. Fish. Bull. 87, 471-495.

Houde, E. D., 2008. Emerging from Hjort's shadow. J. Northwest Atl. Fish. Sci. 41, 53-70.

Hunt, G. L., Coyle, K. O., Eisner, L. B., Farley, E. V., Heintz, R. A., Mueter, F., Napp, J. M., Overland, J. E., Ressler, P. H., Salo, S., 2011. Climate impacts on eastern Bering

Sea foodwebs: a synthesis of new data and an assessment of the Oscillating Control Hypothesis. ICES J. Mar. Sci. 68, 1230-1243.

Hurst, T. P., 2007. Thermal effects on behavior of juvenile walleye pollock (*Theragra chalcogramma*): implications for energetics and food web models. Can. J. Fish. Aquat. Sci. 64, 449-457.

Hurst, T. P., Cooper, D. W., Duffy-Anderson, J. T., Farley, E. V., 2015. Contrasting coastal and shelf nursery habitats of Pacific cod in the southeastern Bering Sea. ICES J. Mar. Sci. 72, 515-527.

Hurst, T. P., Cooper, D. W., Scheingross, J. S., Seale, E. M., Laurel, B. J., Spencer, M. L., 2009. Effects of ontogeny, temperature, and light on vertical movements of larval Pacific cod (*Gadus macrocephalus*). Fish. Oceanogr. 18, 301-311.

Hurst, T. P., Duffy, T. A., 2005. Activity patterns in northern rock sole are mediated by temperature and feeding history. J. Exp. Mar. Biol. Ecol. 325, 201-213.

Hurst, T. P., Moss, J. H., Miller, J. A., 2012. Distributional patterns of 0-group Pacific cod (*Gadus macrocephalus*) in the eastern Bering Sea under variable recruitment and thermal conditions. ICES J. Mar. Sci. 69, 163-174.

Hurst, T. R., Laurel, B. J., Ciannelli, L., 2010. Ontogenetic patterns and temperature-dependent growth rates in early life stages of Pacific cod (*Godus macrocephalus*). Fish. Bull. 108.

Huwer, B., Clemmesen, C., Grønkjær, P., Köster, F. W., 2011. Vertical distribution and growth performance of Baltic cod larvae – Field evidence for starvation-induced recruitment regulation during the larval stage? Prog. Oceanogr. 91, 382-396.

Ikeda, T., Shiga, N., Yamaguchi, A., 2008. Structure, biomass distribution and trophodynamics of the pelagic ecosystem in the Oyashio region, western subarctic Pacific. J. Oceanogr. 64, 339-354.

Illing, B., Moyano, M., Berg, J., Hufnagl, M., Peck, M. A., 2016. Behavioral and physiological responses to prey match-mismatch in larval herring. Estuary Coast Shelf Sci. doi:10.1016/j.ecss. 2016.01.003.

Jenkins, G. P., 1988. Micro- and fine-scale distribution of microplankton in the feeding environment of larval flounder. Mar. Ecol. Prog. Ser. 43, 233-244.

Jordaan, A., Brown, J. A., 2003. The risk of running on empty: the influence of age on starvation and gut fullness in larval Atlantic cod (*Gadus morhua*). Can. J. Fish. Aquat. Sci. 60, 1289-1298.

Jørgensen, C., Opdal, A. F., Fiksen, Ø., 2014. Can behavioural ecology unite hypotheses for fish recruitment? ICES J. Mar. Sci. 71, 909-917.

Kanno, Y., Ueda, Y., Matsuishi, T., 2001. Subpopulations of Pacific cod *Gadus macrocephalus* off the Pacific coast of Northern Japan. Bull. Jpn. Soc. Sci. Fish. 67, 66-77. (in Japanese with English abstract)

Kawauchi, Y., Chimura, M., Mutoh, T., Watanobe, M., Shirakawa, H., Miyashita, K., 2014. Effect of environmental factors and prey species on daytime and nighttime vertical distribution of juvenile walleye pollock in and around Funka Bay. Fish. Sci. 80, 139-149.

Killen, S. S., 2014. Growth trajectory influences temperature preference in fish through an effect on metabolic rate. J. Anim. Ecol. 83, 1513-1522.

Kristiansen, T., Stock, C., Drinkwater, K. F., Curchitser, E. N., 2014. Mechanistic insights into the effects of climate change on larval cod. Glob. Chang. Biol. 20, 1559-1584.

Laurel, B. J., Stoner, A., Ryer, C., Hurst, T., Abookire, A., 2007. Comparative habitat associations in juvenile Pacific cod and other gadids using seines, baited cameras and laboratory techniques. J. Exp. Mar. Biol. Ecol. 351, 42-55.

Laurel, B. J., Hurst, T. P., Ciannelli, L., 2011. An experimental examination of temperature interactions in the match-mismatch hypothesis for Pacific cod larvae. Can. J. Fish. Aquat. Sci. 68, 51-61.

Laurel, B. J., Ryer, C. H., Knoth, B., Stoner, A. W., 2009. Temporal and ontogenetic shifts in habitat use of juvenile Pacific cod (*Gadus macrocephalus*). J. Exp. Mar. Biol. Ecol. 377, 28-35.

Laurence, G. C., 1972. Comparative swimming abilities of fed and starved larval largemouth bass (*Micropterus salmoides*). J. Fish Biol. 4, 73-78.

Letcher, B. H., Rice, J. A., 1997. Prey patchiness and larval fish growth and survival: inferences from an individual-based model. Ecol Modell 95, 29-43.

Li, Z., Yamamoto, J., Sakurai, Y., 2015. Vertical position, specific gravity and swimming ability of Pacific cod *Gadus macrocephalus* yolk-sac larvae reared at four temperatures. Fish. Sci. 81, 883-889.

Lienart, G. D., Mitchell, M. D., Ferrari, M. C., McCormick, M. I., 2014. Temperature and food availability affect risk assessment in an ectotherm. Anim. Behav. 89, 199-204.

Litvak, M. K., Leggett, W. C., 1992. Age and size-selective predation on larval fishes: the bigger-is-better hypothesis revisited. Mar. Ecol. Prog. Ser. 81, 13-24.

McLeod, I. M., Rummer, J. L., Clark, T. D., Jones, G. P., McCormick, M. I., Wenger, A. S., Munday, P. L., 2013. Climate change and the performance of larval coral reef fishes: the interaction between temperature and food availability. Conservation Physiology 1, cot024.

McNamara, J. M., Houston, A. I., 1987. Starvation and predation as factors limiting population size. Ecology 68, 1515-1519.

Miller, T. J., 2007. Contribution of individual-based coupled physical-biological models to understanding recruitment in marine fish populations. Mar. Ecol. Prog. Ser. 347, 127-138.

Moberg, O., Braithwaite, V. A., Jensen, K. H., Salvanes, A. G. V., 2011. Effects of habitat enrichment and food availability on the foraging behaviour of juvenile Atlantic Cod (*Gadus morhua L*). Environ. Biol. Fish. 91, 449-457.

Morioka, T., Kuwada, H., 2002. The upper limit of inhabiting temperature and the diet of juvenile Pacific cod *Gadus macrocephalus* in the northern part of Nanao Bay and its vicinity, Japan. Bull. Japan. Soc. Sci. Fish. 68, 345-350 (in Japanese with English abstract).

Moss, J. H., Farley Jr, E. V., Feldmann, A. M., Ianelli, J. N., 2009. Spatial distribution, energetic status, and food habits of eastern Bering Sea age-0 walleye pollock. T. Am. Fish. Soc. 138, 497-505.

Moss, J. H., Zaleski, M. F., Heintz, R. A., 2015. Distribution, diet, and energetic

condition of age-0 walleye pollock (*Gadus chalcogrammus*) and pacific cod (*Gadus macrocephalus*) inhabiting the Gulf of Alaska. Deep-sea Res. Part II. 132, 146-153.

Munk, P., 1995. Foraging behaviour of larval cod (*Gadus morhua*) influenced by prey density and hunger. Mar. Biol. 122, 205-212.

Munk, P., Kiorboe, T., 1985. Feeding behaviour and swimming activity of larval herring (*Clupea harengus*) in relation to density of copepod nauplii. Mar. Ecol. Prog. Ser. 24, 15-21.

Nakatani, T., Sugimoto, K., Takatsu, T., Takahashi, T., 2003. Environmental factors in Funka Bay, Hokkaido, affecting the year class strength of walleye pollock, *Theragra chalcogramma*. Bull. Jpn. Soc. Fish. Oceanogr. 67, 23-28. (in Japanese with English abstract)

Nicieza, A. G., Metcalfe, N. B., 1997. Growth Compensation in Juvenile Atlantic Salmon: Responses to Depressed Temperature and Food Availability. Ecology 78, 2385-2400.

O'Connor, M. I., Bruno, J. F., Gaines, S. D., Halpern, B. S., Lester, S. E., Kinlan, B. P., Weiss, J. M., 2007. Temperature control of larval dispersal and the implications for marine ecology, evolution, and conservation. Proc. Natl. Acad. Sci. U.S.A. 104, 1266-1271.

Olla, B. L., Davis, M. W., 1990. Effects of physical factors on the vertical distribution of larval walleye pollock *Theragra chalcogramma* under controlled laboratory conditions. Mar. Ecol. Prog. Ser. 63, 105–112.

Orians, G. H., Wittenberger, J. F., 1991. Spatial and temporal scales in habitat selection.

Am. Nat. 137, S29-S49.

Otterlei, E., Nyhammer, G., Folkvord, A., Stefansson, S. O., 1999. Temperature-and size-dependent growth of larval and early juvenile Atlantic cod (*Gadus morhua*): a comparative study of Norwegian coastal cod and northeast Arctic cod. Can. J. Fish. Aquat. Sci. 56, 2099-2111.

Ottmar, M. L., Hurst, T. P., 2012. Thermal effects on swimming activity and habitat choice in juvenile Pacific cod (*Gadus macrocephalus*). Mar. Biol. 159, 2185-2194.

Owens, H. L., 2015. Evolution of codfishes (Teleostei: Gadinae) in geographical and ecological space: evidence that physiological limits drove diversification of subarctic fishes. J. Biogeogr. 42, 1091-1102.

Pepin, P., 1991. Effect of temperature and size on development, mortality, and survival rates of the pelagic early life history stages of marine fish. Can. J. Fish. Aquat. Sci. 48, 503-518.

Perry, A. L., Low, P. J., Ellis, J. R., Reynolds, J. D., 2005. Climate change and distribution shifts in marine fishes. Science 308, 1912-1915.

Platt, T., Fuentes-Yaco, C., Frank, K. T., 2003 Marine ecology: spring algal bloom and larval fish survival. Nature 423, 398-399.

Pörtner, H. O., Farrell, A. P., 2008. Physiology and climate change. Science 322, 690-692.

Puvanendran, V., Brown, J. A., 1999. Foraging, growth and survival of Atlantic cod larvae reared in different prey concentrations. Aquaculture 175, 77-92.

Puvanendran, V., Leader, L., Brown, J., 2002. Foraging behaviour of Atlantic cod

(*Gadus morhua*) larvae in relation to prey concentration. Can. J. Zool. 80, 689-699.

Sakurai, Y., 2007. An overview of the Oyashio ecosystem. Deep-sea Res. Part II. 54, 2526-2542.

Sakurai, Y., Hattori, T., 1996. Reproductive behavior of Pacific cod in captivity. Fish. Sci. 62, 222-228.

Sih, A., 1980. Optimal behavior: can foragers balance two conflicting demands. Science 210, 1041-1043.

Sims, D. W., Wearmouth, V. J., Southall, E. J., Hill, J. M., Moore, P., Rawlinson, K., Hutchinson, N., Budd, G. C., Righton, D., Metcalfe, J. D., 2006. Hunt warm, rest cool: bioenergetic strategy underlying diel vertical migration of a benthic shark. J. Anim. Ecol. 75, 176-190.

Skajaa, K., Browman, H. I., 2007. The escape response of food-deprived cod larvae (*Gadus morhua* L.). J. Exp. Mar. Biol. Ecol. 353, 135-144.

Skiftesvik, A. B., 1992. Changes in behaviour at onset of exogenous feeding in marine fish larvae. Can. J. Fish. Aquat. Sci. 49, 1570-1572.

Sogard, S. M., Olla, B. L., 1996. Food deprivation affects vertical distribution and activity of a marine fish in a thermal gradient: potential energy-conserving mechanisms. Mar. Ecol. Prog. Ser. 133, 43-55.

Sogard, S. M., Olla, B., 1998. Behavior of juvenile sablefish, *Anoplopoma fimbria* (Pallas), in a thermal gradient: Balancing food and temperature requirements. J. Exp. Mar. Biol. Ecol. 222, 43-58.

Sreenivasan, A., Heintz, R., 2016. Estimation of the relationship between growth,

consumption, and energy allocation in juvenile pacific cod (*Gadus macrocephalu*s) as a function of temperature and ration. Deep-sea Res. Part II. 132, 154-161.

Strasburger, W. W., Hillgruber, N., Pinchuk, A. I., Mueter, F. J., 2014. Feeding ecology of age-0 walleye pollock (*Gadus chalcogrammus*) and Pacific cod (*Gadus macrocephalus*) in the southeastern Bering Sea. Deep-sea Res. Part II. 109, 172-180.

Takatsu, T., Nakatani, T., Mutoh, T., Takahashi, T., 1995. Feeding habits of Pacific cod larvae and juveniles in Mutsu Bay, Japan. Fish. Sci. 61, 415-422.

Takatsu, T., Yoshida, Y., Kooka, K., Sugimoto, K., Takahashi, T., 2001. Spatial and temporal distribution of Pacific cod *Gadus macrocephalus* juveniles in Mutsu Bay, Japan. Bull. Jpn. Soc. Fish. Oceanogr. 65, 6-14.

Takatsu, T., Nakatani, T., Miyamoto, T., Kooka, K., Takahashi, T., 2002. Spatial distribution and feeding habits of Pacific cod (*Gadus macrocephalus*) larvae in Mutsu Bay, Japan. Fish. Oceanogr. 11, 90-101.

Theilacker, G. H., Bailey, K. M., Canino, M. F., Porter, S. M., 1996. Variations in larval walleye pollock feeding and condition: a synthesis. Fish. Oceanogr. 5, 112-123.

van Dijk, P., Staaks, G., Hardewig, I., 2002. The effect of fasting and refeeding on temperature preference, activity and growth of roach, *Rutilus rutilus*. Oecologia 130, 496-504.

Vikebø, F., Jørgensen, C., Kristiansen, T., Fiksen, Ø., 2007. Drift, growth, and survival of larval Northeast Arctic cod with simple rules of behaviour. Mar. Ecol. Prog. Ser. 347, 207-219.

Vollset, K., Fiksen, Ø., Folkvord, A., 2009. Vertical distribution of larval cod (*Gadus*

morhua) in experimental temperature gradients. J. Exp. Mar. Biol. Ecol. 379, 16-22.

Vollset, K., Catalán, I., Fiksen, O., Folkvord, A., 2013. Effect of food deprivation on distribution of larval and early juvenile cod in experimental vertical temperature and light gradients. Mar. Ecol. Prog. Ser. 475, 191-201.

von Herbing, I., 2002. Effects of temperature on larval fish swimming performance: the importance of physics to physiology. J. Fish Biol. 61, 865-876.

von Herbing, I. H., Gallager, S., 2000. Foraging behavior in early Atlantic cod larvae (*Gadus morhua*) feeding on a protozoan (*Balanionsp*.) and a copepod nauplius (*Pseudodiaptomussp*.). Mar. Biol. 136, 591-602.

von Herbing, I. H., Boutilier, R., Miyake, T., Hall, B., 1996. Effects of temperature on morphological landmarks critical to growth and survival in larval Atlantic cod (*Gadus morhua*). Mar. Biol. 124, 593-606.

Werner, E. E., Gilliam, J. F., Hall, D. J., Mittelbach, G. G., 1983. An experimental test of the effects of predation risk on habitat use in fish. Ecology 64, 1540-1548.

Wildhaber, M. L., Crowder, L. B., 1990. Testing a bioenergetics-based habitat choice model: bluegill (*Lepomis macrochirus*) responses to food availability and temperature. Can. J. Fish. Aquat. Sci. 47, 1664-1671.

Yin, M., Blaxter, J., 1987. Temperature, salinity tolerance, and buoyancy during early development and starvation of Clyde and North Sea herring, cod, and flounder larvae. J. Exp. Mar. Biol. Ecol. 107, 279-290.

Yoo, H. K., Yamamoto, J., Saito, T., Sakurai, Y., 2014. Laboratory observations on the vertical swimming behavior of Japanese common squid *Todarodes pacificus*

paralarvae as they ascend into warm surface waters. Fish. Sci. 80, 925-932.