

博士論文（要約）

**Habitat use and behavior of
Lates japonicus in Shimanto Estuary,
an endangered endemic fish in Japan**

(日本の絶滅危惧固有種アカメ *Lates japonicus* の
四万十川河口域における生息場利用と行動)

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サラ ゴンザルボ マロ
Sara Gonzalvo Marro

THE UNIVERSITY OF TOKYO

Graduate School of Agriculture and Life Sciences

Department of Aquatic Bioscience

Laboratory of Behavior, Ecology and Observation Systems

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*To my family and friends,
for encouraging me all the way here.*

*A special thought for
my loving parents and sisters,
whose unconditional support
made this day possible.*

Muchísimas gracias a todos.

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Abstract

Lates japonicus (Katayama & Taki, 1984), commonly known as the Japanese seabass or Akame in Japan, is a predatory species endemic of the estuaries and coastal waters on the Pacific coast of south-east Japan (Iwatsuki et al., 1993). This rare species is listed in the Red Book of endangered species of the Ministry of Environment of Japan as a Threatened IB species (correspondent to IUCN's Endangered, EN, category). *L. japonicus* is a game fish to reach sizes near 140 cm in total length (TL) and weight 39 kg (IGFA, 2016), often caught in the estuaries of big rivers in Kochi Prefecture.

One of the main areas where this species is targeted by catch-and-release sport anglers is Shimanto Estuary, Shikoku Island. Establishment of management plans in Shimanto Estuary and other areas for *L. japonicus* is necessary to conserve the remaining populations of this species while allowing a sustainable development of estuarine and coastal areas. Very few studies have been conducted on this species and little is known about its ecology. For establishing integrated management and conservation measures, information on the life history, habitat use and migrations of *L. japonicus* is necessary. This study aims to elucidate habitat use and behavior of this species at different life stages in Shimanto Estuary.

The microstructure and microchemistry of otoliths was used to reconstruct the life history of *L. japonicus* in Shimanto Estuary. To minimize the number of fishes sacrificed for their otoliths, frozen samples donated by local anglers and aquariums were also used. The Sr/Ca on the otoliths of juvenile fishes collected on seagrass beds, and in fishes cultured in brackish water tanks (salinity of 17-19) was used to identify threshold values for estuarine waters. Values over and below the thresholds of brackish water were allocated to seawater and freshwater respectively. The threshold values were used to analyze hatching areas and movements inside and outside the estuary at juvenile, young and adult life stages.

Results of the analysis of the otoliths suggested that most of the individuals hatched in the estuary, where brackish water was distributed. The levels of Sr/Ca in the otoliths of juvenile fishes caught in seagrass beds incremented towards the edge, and was linked with an increment in ambient salinity. Counting otolith's daily rings and relating the age of the fish with its TL, the increment was calculated to have started between the 11th and 16th day of life, at sizes near 5.3- 7.9 mm TL. This increment in the ambient salinity water was linked with the recruitment to the seagrass beds where fishes were caught, located at higher salinity waters on the bottom of the estuary.

In the otoliths of young and adult fishes the levels of Sr/Ca in the otolith tended to decrease as fishes aged, which suggested a movement outside the seagrass beds and towards upper stream areas. However, Sr/Ca levels on the otoliths remained always within the range allocated for estuarine waters, which suggested that all analyzed samples had an estuarine life history, being born in the estuary and remaining on it without any long term residence shift to freshwater or coastal areas. The analyzed individuals can be considered as estuarine residents since they spent their whole life in estuarine brackish waters.

Otolith analysis can't discriminate short term movements to freshwater or coastal areas. To obtain habitat use and behavior information on a short scale, acoustic telemetry methodology was applied. Movements of *L. japonicus* in Shimanto Estuary were monitored using acoustic transmitters and receivers deployed in fixed arrays at selected points. The first tracking experiment was conducted from winter of 2014 to spring of 2015, using four 42.5±0.5 cm TL aquarium-reared individuals. The fish belonged to a restocking project for *L. japonicus* in Shimanto Estuary conducted by the Akame Gakuyukan, a local aquarium in Shimanto City. Anaesthetized fishes were inserted with a Vemco V9P transmitter in their intra-peritoneal cavity, and their movements tracked with nine acoustic receivers.

The results of this tracking study showed that 100% of the individuals survived during the first month, and at least 75% of them did for six months after releasing. Individuals remained in the estuary in proximity to the seagrass beds located in the small streams on both sides of the main stream of the estuary. Diurnal movements between residences following daylight were detected for two fishes, and those following the tides in another one. It suggested that young *L. japonicus* selected habitats strongly linked to the presence of seagrass beds. The great survival rate and estuarine fidelity of the released individuals showed that stock enhancement of *L. japonicus* releasing wild-captured aquarium-reared fishes might be a successful measure to increase the number of *L. japonicus* in Shimanto Estuary.

To analyze the behavior and habitat use of wild adult *L. japonicus*, a second tracking experiment was conducted between mid-June and early October of 2016, covering the whole spawning season of *L. japonicus*, estimated between late June and August. Five individuals between 69 and 92 cm TL were captured in Shimanto Estuary and tagged externally using a Vemco V13P acoustic transmitter attached to a modified dart tag. The individuals were tracked with nine acoustic receivers deployed in fixed stations along the estuary, seven of which were retrieved on the 13th -15th of October of 2016.

Apparently, some of the adults of *L. japonicus* tracked concentrated in the upper reaches of the estuary, close to the limit of the incursion of the salt wedge. These individuals remained in the upper estuary during the whole tracking period except two fishes, which migrated downstream to the estuary mouth. This migration towards the estuary mouth observed for two different individuals occurred in July for one fish and in August for the other, and was severely influenced by lunar phase. It seems that this downstream migration is related to spawning, since a very similar behavior has been observed in the related species *L. calcarifer* (Moore, 1980; Moore, 1982; Davis, 1986; Garcia, 1992).

The migration towards the estuary mouth started during full moon periods. The two individuals disappeared from the range of the receivers during the following last quarter moon. The disappearances continued for three consecutive nights. One individual returned to the estuary and again disappeared for another three consecutive nights during the same last quarter moon period, whilst the other did it only once. After returning to the coverage, one individual remained in Shimanto Estuary, while the other left and was found inhabiting a nearby estuary located 30 km south of Shimanto River along the coastline.

Reports on the spawning migration from freshwater to the estuary mouth and nearby coastal waters of *L. calcarifer* supports that the migration in *L. japonicus* might be for spawning. In Shimanto Estuary, not all of adult *L. japonicus* spawn every year, even when they are potentially capable according to size, and they don't do it all at once. Spawning is synchronized with last quarter moon periods, occurring several times during the spawning season. Spawning grounds are not identified but very close to the estuary mouth. After spawning, spawned individuals may re-enter Shimanto Estuary or move to nearby estuarine systems.

In order to investigate the habitat use of adults of *L. japonicus* into more detail, the data collected with an animal-borne digital still-camera logger (DSL) attached to an 89 cm TL wild *L. japonicus* in summer of 2009 was analyzed. The analysis of the images recorded during the six hours of experiment revealed adults of *L. japonicus* forming shoals. The experiment individuals rapidly found a shoal of *L. japonicus* after released, which suggests that individuals *L. japonicus* form groups frequently. The shoals were detected in July on the upper reaches of the estuary, and consisted of individuals of apparently similar sizes to the released fish.

This study revealed the great importance that estuarine waters have for this species at all life stages. In Shimanto Estuary, all of their life cycle seems to be strongly linked to the brackish estuarine waters. Spawning may have occurred close to the estuary mouth and larvae hatched out in the estuary. Juveniles were found in estuarine seagrass nurseries, and young fishes shifted residences in areas close to seagrass beds. Adult fishes were found in the upper reaches of the salt wedge, and some of them remained for many years inside the estuary. Two tracked adult individuals, migrated to lower reaches of the estuary and disappeared for three days. This migration probably relates to spawning.

Abstract

The importance that residences located in the estuary have for *Lates japonicus* at many life stages is conspicuous. To protect the remaining populations of this species in Shimanto Estuary and create comprehensive management actions, all the estuary must be taken into account. Restocking programs might provide a solution to increase the stock of this species in the estuarine waters. However, it is imperative to protect key habitats, especially seagrass beds, necessary for the survival of several life stages of *L. japonicus*.

Chapter I

Introduction

Lates japonicus, a rare fish of Japan

Lates japonicus (Katayama & Taki, 1984) called Akame in Japanese and commonly known as the Japanese seabass or Japanese lates in English, is a top predatory fish endemic of the estuarine and coastal waters surrounding Kyushu and Shikoku islands (Iwatsuki et al., 1993). This species was first described by Katayama and Taki (1984), previously thought to be a variety of *Lates calcarifer* (Bloch), an Indo-Pacific species distributed in Asia and Australia called seabass or barramundi. Most of the species of the genus *Lates* are found at rivers, estuaries and coastal areas in tropical waters of Africa and Asia (Greenwood, 1976). However, *L. japonicus* is the only exceptional species among the genus living outside the tropical area, and is distributed in the warm temperate area (Spalding et al., 2007) of the Pacific coast of southern Japan.

Species of the genus *Lates* have a typical percoid shape with spiny fins and a compressed body, deepest at the origin of a two-part dorsal fin. The head is moderately acute with an oval eye and an oblique mouth with a lower jaw projecting beyond the upper one when closed (Katayama & Taki, 1984; Pethiyagoda & Gill, 2012). The morphology of *L. japonicus* is similar to that of *L. calcarifer* and both species have eyes of a shiny ruby-pink color, a possible adaptation to finding prey in low light conditions, which gives the common name to *L. japonicus* (Akame in Japanese means “red eye”). Katayama and Taki (1984) described that: “In *L. japonicus* the body is deeper, and the third dorsal and second anal spines are longer in relation to both standard length and head length. The third dorsal spine is longer than the pelvic fin in *L. japonicus* but shorter in *L. calcarifer*, and the second anal spine is longer than the third in *L. japonicus* but much shorter in *L. calcarifer*” (Figure 1.1).

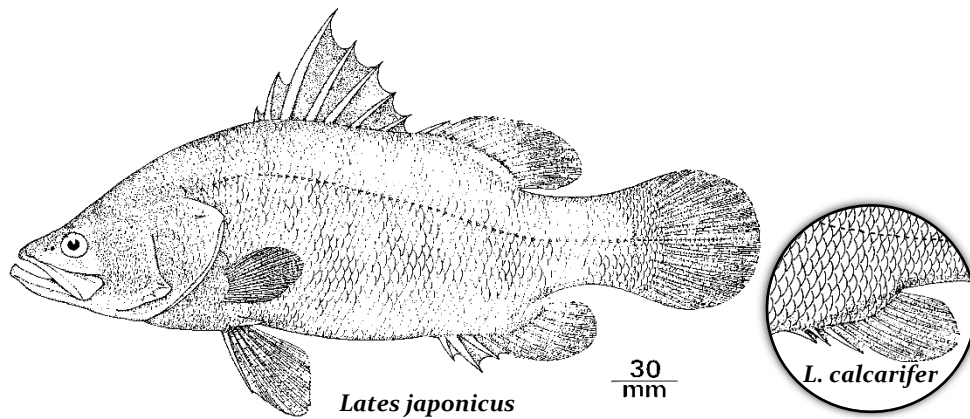


Figure 1.1. Illustration of a *Lates japonicus* and the anal fin of *Lates calcarifer* extracted from “*Lates japonicus*, a New Centropomid Fish from Japan” of Katayama and Taki (1984)

L. japonicus is a rare fish listed as endangered since 1992 (Asahina et al., 1992) and categorized as Threatened IB^{*1} in the Red Data Book of the Ministry of Environment of Japan of 2015. This species remains quite unknown nowadays, with only a few scientific communications and reports published. Iwatsuki et al. (1993) described the distribution of *L. japonicus*, which is limited to the southern Pacific coast of Japan (Figure 1.2). The authors postulated that relatively high minimum water temperatures during winter and the presence of big rivers might condition its distribution.

Kinoshita et al. (1988) described the size and morphology as well as the seasonal occurrences of larvae and juvenile of *L. japonicus* in Shimanto Estuary. The authors estimated that the spawning season of this species occurs once a year, between late June and August based on the size and seasonal occurrences of larvae and juveniles. The same authors postulated that spawning likely occurs in coastal waters nearby the estuary.

Iwatsuki et al. (1994) found a matured female of *L. japonicus* in the estuarine waters of Oyodo River in Miyazaki Prefecture (Kyushu Island). Observing the maturity condition of its ovary and taking the time of its capture into consideration, the authors stated that their observations supported the hypothesis of Kinoshita et al. (1988) on the spawning season of *L. japonicus* occurring probably once a year after the onset of the rainy season. They speculated that spawning may occur inside the estuarine waters. If this is true, the spawning pattern of *L. japonicus* is very similar to that of *L. calcarifer* reported in several populations (e.g. Grey, 1987). The latter species is known to spawn once a year during the rainy season (Davis, 1985) in estuaries or coastal waters near river mouths (Grey, 1987).

^{*1} Threatened IB corresponds to the IUCN’s category of Endangered (EN), and stands for species that face a risk of extinction in the wild in the near future but are not as endangered as those listed in Threatened IA (correspondent to IUCN’s Critically Endangered, CR).

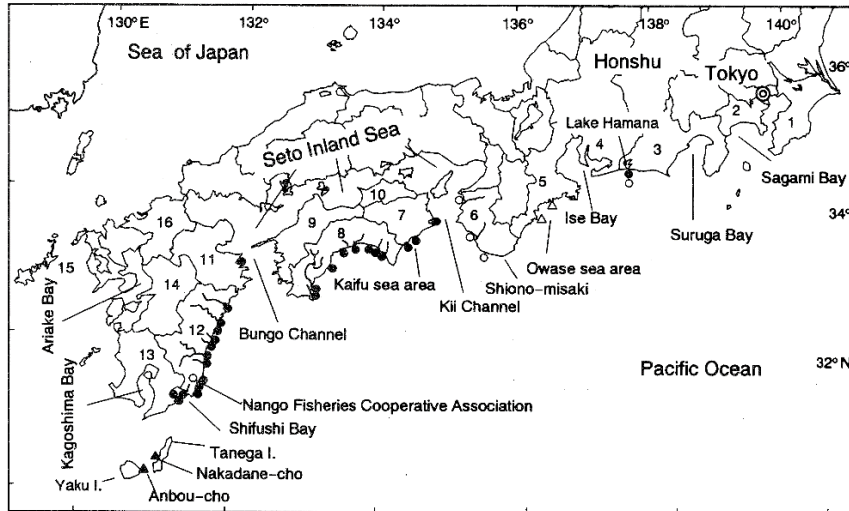


Figure 1.2. Map showing the distribution of *Lates japonicus* in Japan extracted from “Distribution and Fluctuations in Occurrence of the Japanese Centropomid Fish, *Lates japonicus*” of Iwatsuki et al. (1993). Distribution was established according to specimens and photographs (●), literature records and large set net catches (○), personal communication (△), and local information of presumed distribution (▲). Prefectures are indicated in numbers: 1-Chiba, 2-Kanagawa, 3-Shizuoka, 4-Aichi, 5-Mie, 6-Wakayama, 7-Tokushima, 8-Kochi, 9-Ehime, 10-Kagawa, 11-Oita, 12-Miyazaki, 13-Kagoshima, 14-Kumamoto, 15-Nagasaki and 16-Fukuoka.

Tashiro and Iwatsuki (1995) revealed that the feeding activity of *L. japonicus* is closely related to temperature, which makes the species to stop feeding below water temperatures of 16°C. The feeding behavior of adult *L. japonicus* was studied in detail by Tanoue et al. (2012) confirming that feeding was performed using a powerful suction, similar to the feeding system of *L. calcarifer* and *L. niloticus*. Tanoue et al. (2012) also detected feeding events of wild and captive individuals released in Shimanto Estuary. The main feeding activity occurred in deeper areas of the estuary, both at night and during daytime.

L. japonicus can reach 138 cm in total length (TL) and weigh 39 kg (IGFA, 2016). Uchida (2005) reported that juveniles of *L. japonicus* are found in seagrass beds and estimated that they recruit in the seagrass nurseries several times during the spawning season at larvae stages. This resembles the reported use of seagrass beds as nurseries of juveniles of *L. calcarifer* where individuals recruit at larvae stages (Moore, 1982).

Uchida (2005) speculated that juveniles of *L. japonicus* remain in the nurseries for feeding on crustaceans and fishes until the onset of the next rainy season. It has been reported that the juveniles of *L. calcarifer* leave the nurseries after the rainy season is over, migrate to upper reaches of the estuary and freshwater systems for passing their main growing phase (Russell & Garret, 1985), and remain there until they attain sexual maturity (Russell & Garret, 1988; Grey, 1987). Upstream migration of young-of-the-year and juveniles has not been studied for *L. japonicus*.

L. calcarifer mature first as males when they reach near 60 cm TL, and undergo a sex-change at sizes over 80 cm TL (Moore, 1979). The change of sex from male to female depending on growth is known as a protandry hermaphroditism (e.g. Moore, 1979). After maturation, adults of *L. calcarifer* move to spawning grounds often located close to estuary mouths, where many adults remain after spawning (Davis, 1986). Therefore, *L. calcarifer* belongs to the category of catadromous fishes, which migrate to estuary mouths or coastal waters for spawning after maturation (e.g. Myers, 1949). Among the over 30000 species of fishes of the world, only about 250 species are considered as diadromous (Miller, 2016). Although *L. japonicus* may morphologically and ecologically resemble *L. calcarifer*, it has not been verified whether *L. japonicus* is a catadromous fish or not.

A recent DNA analysis revealed a severely depleted genetic diversity and a possible fragmented population structure in *L. japonicus* (Takahashi et al., 2015). Takahashi et al. (2015) estimated that populations of *L. japonicus* in different coastal and estuarine waters might be isolated from each other acting as independent breeding groups. This type of structure had been reported in some groups of *L. calcarifer*, of which the management strategy differs from that of other populations consisting on a single population spread along a coast and its estuaries (Salini & Shaklee, 1988).

L. japonicus is targeted by not commercial fishermen but amateur anglers who enjoy the catch-and-release sport on this game fish. This type of sport fishing doesn't necessary cause direct mortality but can have a negative impact through damages in angled fishes (e.g. Philipp et al., 1997). Estuaries where *L. japonicus* are caught are highly productive areas (Whitfield, 1997; Able, 2005) hosting many fish species and including important habitats used as spawning or nursery grounds. However, estuaries are perturbed by human direct impacts, such as construction of ports, breakwater and reclamation, as well as by indirect impacts from the concentration of pollutants from land and economic activities including ship transports, industries, and construction of residences in watershed areas (e.g. Edgar et al., 2000). In addition to any angling threat, *L. japonicus* is vulnerable to the human impacts on estuaries.

Our world has been facing an alarming extinction rate of species in the last decades and arguably aquatic life has been the most affected (e.g. Ricciardi & Rasmussen, 1999). Most part of the world's coastline has been modified to some degree, and almost all river and estuarine systems have been touched by the consequences of human activities. Human disturbances on estuaries are often a major cause for the decline fish populations. However, degrees of human impacts on species living in the estuary are influenced by the dependency of each species on estuarine habitats which may change along their life (e.g. Able, 2005). The type of conservation measures must be suitable for each species.

To establish coherent management plans for the necessary conservation and sustainable use of biological diversity (CITES, 2011), detailed information on the ecology and behavior of species is required. In order to preserve *L. japonicus* in Japan, it is indispensable to reveal its life history, ecology and behavior, for designing conservation measures for this extremely unknown species.

The study of fish otoliths

Otolith analysis is a technique used since the mid-twentieth century to identify age, growth and population structure of fish species (e.g. Campana 2005). Otoliths are calcified structures barely affected by metabolic processes that increase in size due to the deposition of elements, which ratio can reflect environmental conditions of the ambient water of a fish, such as salinity or temperature (Campana & Thorrold, 2001; Yokouchi et al., 2011; Amano et al., 2013). Otoliths are formed before hatching and grow daily, depositing new layers of materials on the outer surface (Campana & Neilson, 1985).

Otoliths can provide a historical record of environmental conditions that a fish was exposed to during its life (Campana, 1999). Microstructure studies on otolith ring marks have been successfully used to age fishes accurately (e.g. Campana & Neilson, 1985; Campana, 2005). Since the late 1990s, studies on the microstructure and microchemistry of the daily growth increments of otoliths have successfully unveiled early life history of a fish, including dates of hatching and duration of larvae stages, and their relation with ambient conditions (e.g. Anderson & Dalley, 2000; Takahashi et al., 2001; Pasten et al., 2003).

Several microchemistry analyses on fish otoliths showed that the ratio of the elements strontium and calcium (Sr/Ca) along an otolith transect can reveal the salinity of the ambient water to which a fish was exposed to along its life, and be used for reconstructing migration history of diadromous fishes (e.g. Tsukamoto & Arai, 2001; Elsdon & Gillanders, 2003; Gillanders, 2005). This type of analysis was successfully used to resolve important questions regarding the life history of *L. calcarifer* (e.g. Cappelletti et al., 2005; McCulloch et al., 2005).

Using fine-scale instruments for microchemistry and microstructure analysis of fish otoliths, it is possible to estimate periods when a fish migrated from one habitat to another with a different salinity (Elsdon & Gillanders, 2003). Since elements in the otolith remain unchanged after their deposition (Campana, 1999), the analysis of chemical composition and structure of otoliths provides means to reconstruct the whole life history of a fish including hatching and larvae stages.

There is a reported time lag between an environmental change in ambient water salinity around a fish and its reflection on the otolith (e.g. Yokouchi et al., 2011). After a fish is exposed to a different salinity environment, it may take up to ten days for the otolith to start reflecting the change in the Sr/Ca ratio, and more than 20 days for the Sr/Ca ratio of the otolith to stabilize (Elsdon & Gillanders, 2005; Yokouchi et al., 2011). In consequence, it is difficult to detect short-term migrations of fish species at particular life stages.

Monitoring and tracking aquatic wildlife

It is complicated to study the behavior of aquatic animals because water environments prevent scientists from directly observing them. Methods generally used for tracking and monitoring free-living aquatic animals in their natural habitats (e.g. Davis et al., 1999) are based on the use of acoustic telemetry devices and data-loggers (Figure 1.3). Miniaturization of devices including improved downsized sensors permit us to broaden the type of studies on behaviors of aquatic animal species that can be conducted at different life stages (Cooke et al., 2012). The technique of using acoustic telemetry devices to localize and monitor aquatic animals is frequently referred as biotelemetry (Cooke, 2008).

A biotelemetry system consists of a transmitter attached to an animal, which records information and emits it on an acoustic signal, and one or more distanced receivers collecting the signals and storing the data (Cooke, 2008). A data-logger system consists of a data-logger device attached to an animal, able to record and store the information on environmental parameters and accelerations (Boyd et al., 2004). Data-loggers are often deployed along with detaching and recovery systems, which respectively release the logger from the animal at a scheduled time and emit signals after its detachment (Watanabe et al., 2008). Data is stored on the device and is downloaded from the recaptured data-logger.

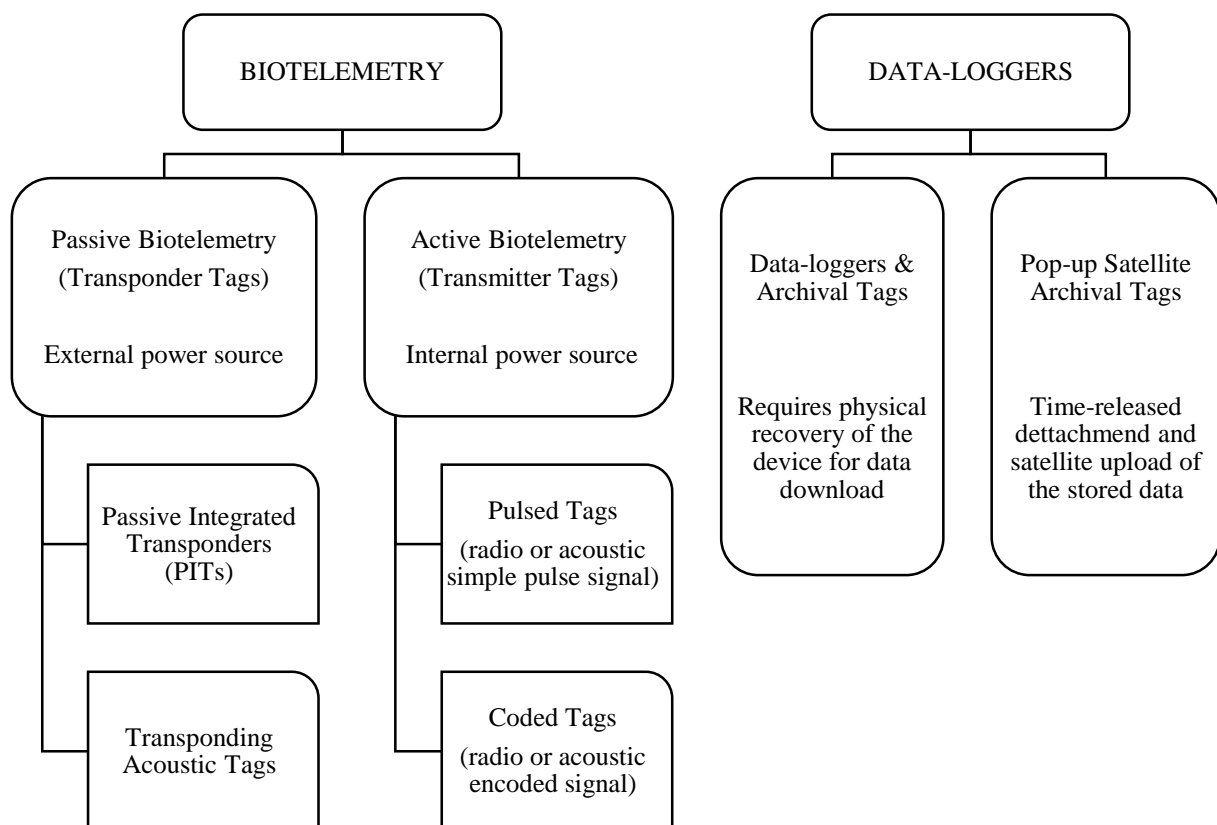


Figure 1.3. Classification of the main remote tracking techniques for aquatic animals (following Thorsteinsson et al., 2002; Cooke et al., 2012)

In the late 1980s, acoustic transmitters and receivers evolved to emit and decode more sophisticated acoustic signals, which resulted in the coded tags (Cooke, 2008). Coded tags allow individual identification of tagged animals, permitting researchers to study individual and collective behaviors of animals. In freshwater systems, tracking of acoustic coded transmitters had successfully disclosed migration patterns in several diadromous species, such as salmonids (e.g. Eiler, 1995; Melnychuk et al., 2007) and eels (e.g. Behrmann-Godel & Eckmann, 2003).

Internal and external attachments are possible for most types of transmitters (Figure 1.4) and they present advantages and disadvantages. Gains of external tagging are no or fewer use of anesthetics and a short handling period of the animal to be attached with the device. The main disadvantage of this method is the risk of device loss since it is exposed to the outside of the body of the animal. On the other hand, internal tagging reduces considerably device loss, but it requires implantation of the transmitters into body cavities, with the consequent surgical manipulation and anaesthetization of the animal. The size and life stage of the target animal needs to be taken into account for selecting the attachment method, since the behavior of tagged fishes can be affected by the type of transmitter and the tagging process (e.g. Mellas & Haynes, 1985; Moore et al., 1990).

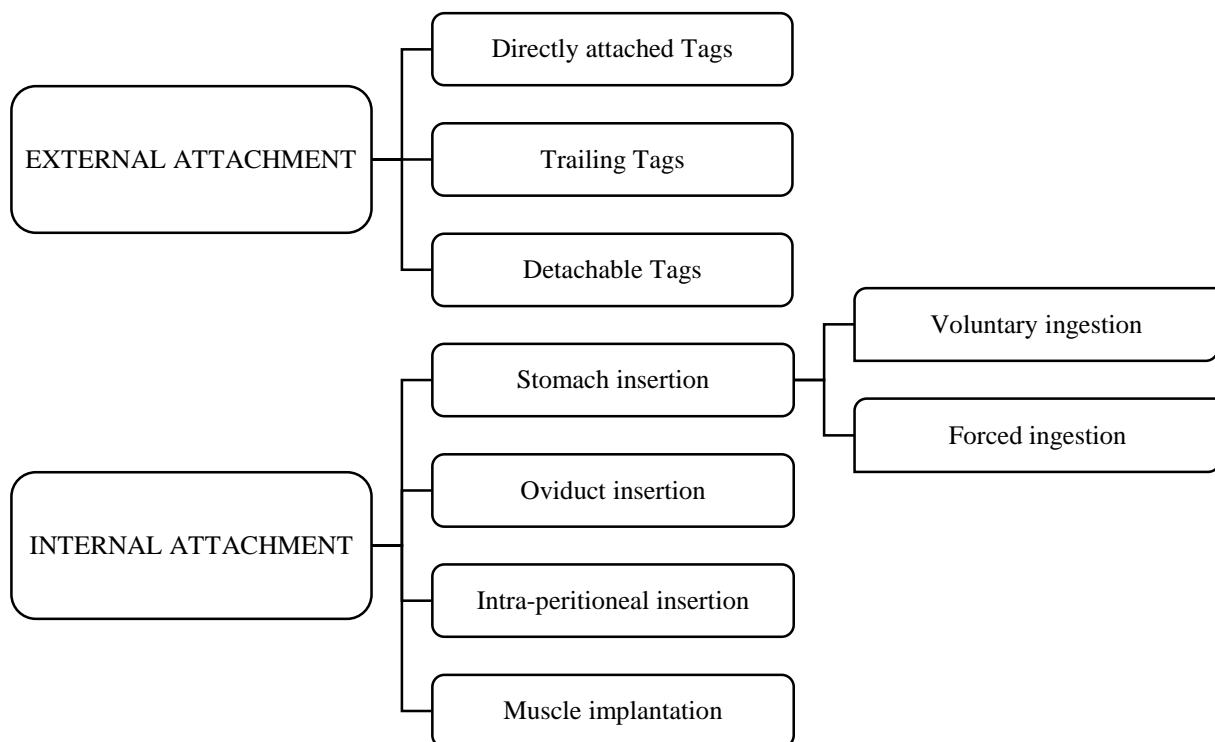


Figure 1.4. Main types of attachment systems of acoustic or electronic transmitters and transponders to animals (FAO Workshop Report, 2001).

There are a few disadvantages in the use of telemetry and logger devices for the study of fishes in rivers and estuaries. Very shallow waters and high water flows prevent acoustic tracking (Stasko & Pincock, 1977). Water turbidity can negatively impact the performance of acoustic devices (Stuehrenberg et al., 1990). The type and size of devices deeply affect the range of signal reception. Because big acoustic transmitters are often powered with long lasting batteries, they emit stronger signals that can be detected at longer ranges, but they can't be used in smaller sizes including individuals at early juvenile stages.

Biotelemetry and data-logger studies are often limited in time, since long-term deployment of receiver arrays and monitoring of tagged fishes is a costly process, and internally powered transmitters are limited by their battery life. Short-term studies are suited for surveying many kinds of interim behaviors and for understanding habitat use and migration at particular seasons. But for long-term understanding, biotelemetry and data-logger systems alone might not be sufficient. In the case of long-living estuarine species long-term observation is necessary. Integration of different types of studies can fulfill gaps intrinsic to each of the used methods and provide a broader view of a species for a better understanding of its behavior and ecology.

For the extensive study of *L. japonicus*, a combination of methods including biotelemetry, data-loggers and otolith studies shall give prospective results. Short-term studies on the behavior, migrations and identification of daily residences of this species might reveal important behavior traits and ecological requirements on a daily scale at different seasons. Long-term otolith studies focusing in shifts between estuarine and coastal habitats can reveal the dependence of this species to the estuary at different life stages, and the moment in their development when important changes in habitats occur. This combination presents an optimal choice for a comprehensive study of the habitat use and behavior *L. japonicus*.

Purpose of the study

From the several estuaries and coastal areas where *Lates japonicus* species is distributed, Shimanto Estuary is arguably the most famous among sport anglers. In Shimanto Estuary, catch-and-release sport fishing of this fish is not only an important economic activity, but also a motivation for the protection of this endangered species. The importance of this endemic fish for local communities in Shimanto Estuary is notorious and has encouraged the creation of local conservation measures carried privately in the aquarium facilities of the Tombo Shimanto Gakuyukan, frequently known in the area as the “Shimanto Gakuyukan” or “Akame Gakuyukan”. The activities carried out on this facility lack the support of scientific studies to evaluate their impact on the recovery of populations of this fish.

For assessing suitable protection strategies for *L. japonicus* we need to understand the relationship between this species and Shimanto Estuary, identify the particular life stages strongly linked to estuarine waters, the timing when changes in habitat occur, as well as particular behavioral traits related with migration and selection of residences. To understand all of these concerns, information on the habitat use and behavior of this species becomes necessary. The aim of this dissertation is to study several aspects of this species in one of its main residence areas, in Shimanto Estuary, for establishing management strategies suitable for its protection.

Shimanto Estuary provides an excellent frame to conduct studies on this species, as there is a local motivation to protect this endangered fish and several unregulated activities on this species are being carried out. To achieve a comprehensive study on this species in Shimanto Estuary, a combination of methods will be used as means to discern its behavior and habitat use at different life stages. The studies presented on this dissertation were focused on Shimanto Estuary, using individuals captured within the limits of the estuary between 2009 and 2016.

Experiments conducted between 2014 and 2016 were personally designed and directed and the results of the data are presented in chapters two to five. Additional data collected in 2009 with data-loggers was personally analyzed and is presented in chapter six. Studies were based on the otolith microstructure and microchemistry and acoustic biotelemetry tracking and animal-borne camera logger surveys for a comprehensive understanding of *Lates japonicus* in Shimanto Estuary.

Chapter II

Environmental conditions on the study site

Introduction

The study site selected to conduct studies on *Lates japonicus* was Shimanto Estuary, one of the most famous spots for sport fishing of this fish in Japan (Kinoshita et al., 1988). Shimanto Estuary is located in the mouth of Shimanto River, in Kochi Prefecture, Shikoku Island, facing the Pacific Ocean (Figure 2.1). Shimanto River flows along 196 km without dams and big cities in its watershed, and is often referred as the “last pristine river of Japan” (JNTO, 2016). Shimanto River falls into Tosa Bay, and the salt wedge usually invades over 6 km upstream from the river mouth (Fujita et al., 2002; Inouchi et al., 2006). In Shimanto Estuary, water temperature and salinities can greatly vary with depth and change among seasons (e.g. Inouchi et al., 2006).

The main stream of Shimanto Estuary is formed by Shimanto River and has bottom depths near 4 m in most areas and maximum bottom depths over 15 m. The width of the stream increases notably, from no more than 200 m in the upper reaches of the estuary to over 500 m near the river mouth. Three smaller rivers, Ushiro River, Nakasuji River and Takeshima River, join Shimanto River at 7 km, 4 km and 200 m upstream of the river mouth, respectively (Figure 2.1). In its lower reaches, the shallow Takeshima River flows gently and is partially covered with seagrass beds (Figure 2.1). Seagrass beds in Shimanto Estuary are composed of only *Zostera japonica* Miki (Fujita et al., 2002) and represent the main nursery for *L. japonicus* in Shimanto Estuary (Kinoshita et al., 1988).

A small channel appears inside main stream of the estuary approximately 3 km upstream of the river mouth, where an island-like formation called “Ohshima” and “Ohshima Channel” are distributed (Figure 2.1). Similar to Takeshima River, in this shallow channel currents flow gently, and its bottom is mostly covered with seagrass beds. The seagrass beds of Ohshima Channel and Takeshima River are the main capture areas for juveniles of *L. japonicus* in Shimanto Estuary (Kinoshita et al., 1988; Figure 2.1).

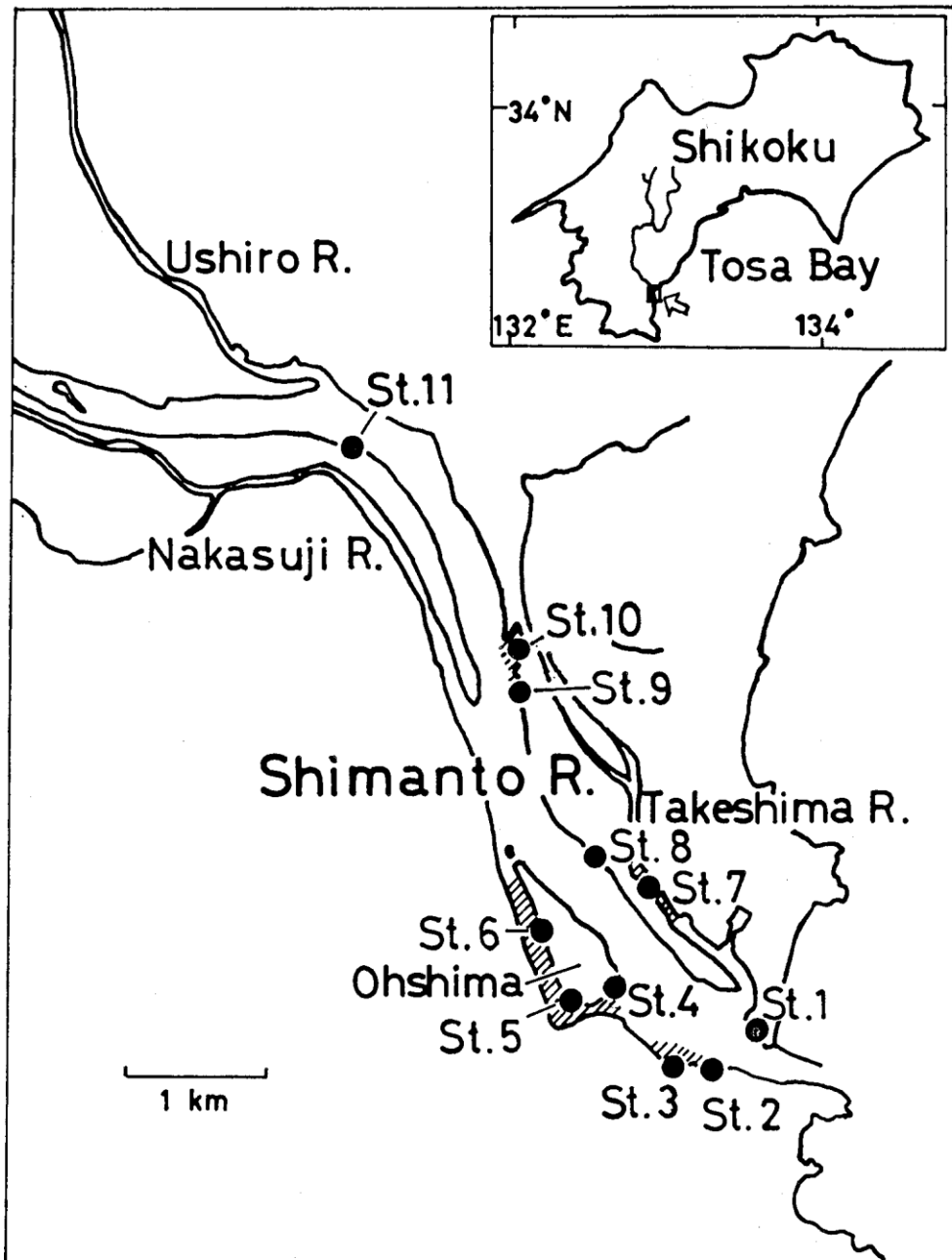


Figure 2.1. Map of Shimanto Estuary extracted from Kinoshita et al. (1988). Shaded areas correspond to seagrass beds areas and closed circles to stations where net captures were taken to evaluate the distribution of larvae and juveniles of *L. japonicus* in Shimanto Estuary.

Materials and Methods

To identify the limits of the estuary (Day, 1989) CTD measurements were conducted at 69 stations from the river mouth to 9 km upstream from the mouth and in the side branches of the estuary in January 29th 2015, and at 18 stations on August 2nd 2016 (Figure 2.2). Measurements were taken sequentially during the same morning, starting near the estuary mouth and ending at the upper reaches of the estuary, where measurements were taken during high tides.

At each station, a CTD profiler (Compact-CTD Lite, JFE Advantec Co., Ltd.) was lowered from the boat and the data compiled in sheets to be integrated in Ocean Data View software. Bottom substrate types were recorded with an action camera (GoPro Hero 4+) attached to the CTD profiler lowered from the boat. The presence of seagrass beds on the estuary was confirmed using the captions of the action camera and through direct observation from the boat and shore areas (Figure 2.2).

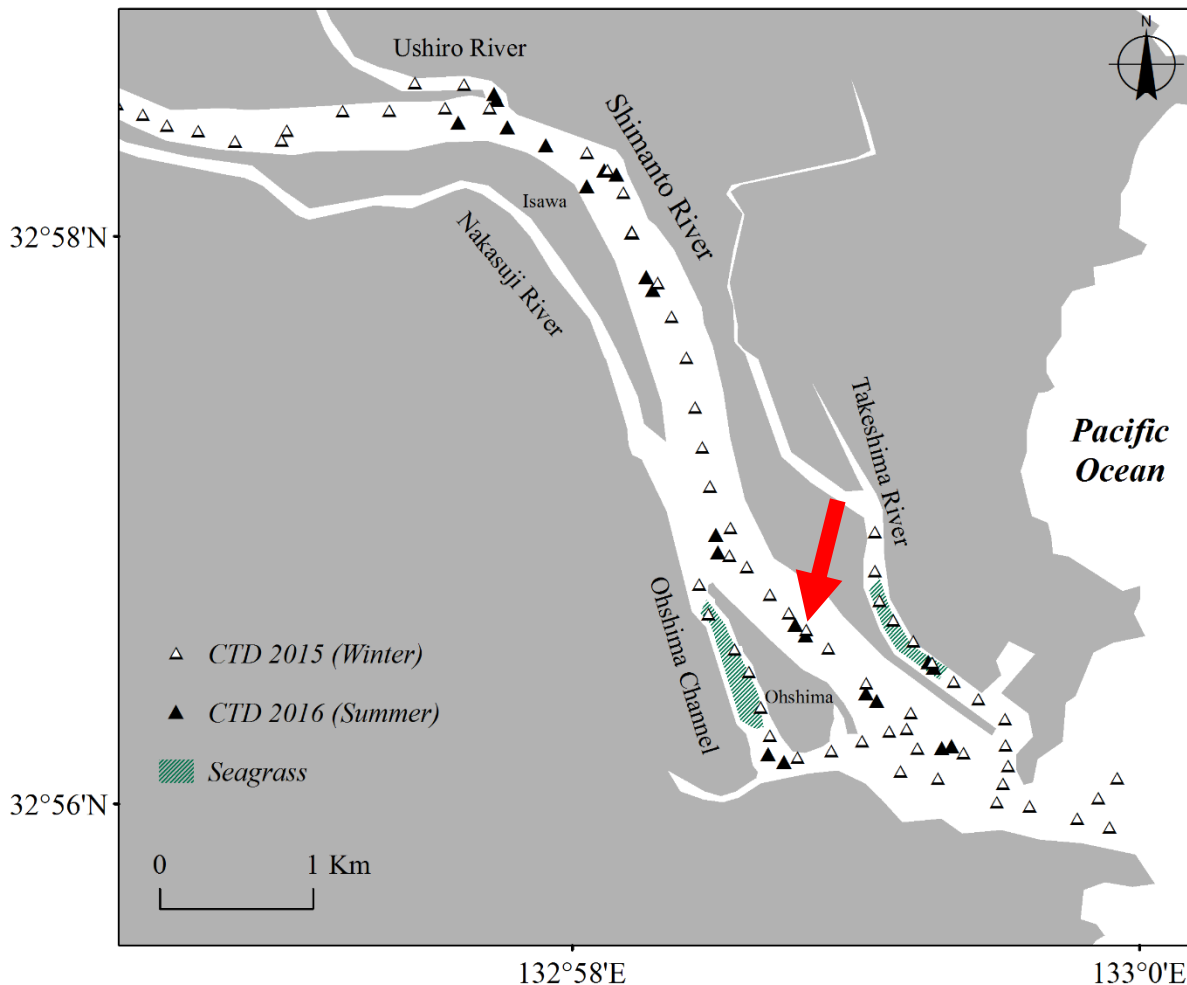


Figure 2.2 Map of Shimanto Estuary showing the stations where CTD measurements were taken in January 29th 2015 (Δ) and August 2nd 2016 (\blacktriangle). Shaded green areas correspond to seagrass beds. A red arrow marks the location used to compare salinity and water temperature profiles between summer and winter.

Results and Discussion

Both observations from the shore and with the recording of the lowered camera during winter of 2015 and summer of 2016 confirmed the presence of broad seagrass bed areas (Figure 2.3) distributed in Ohshima Channel and Takeshima River (Figure 2.2).



Figure 2.3 A caption of the seagrass bed of Ohshima Channel extracted from a video recording of the action camera taken in August of 2016.

CTD profiles along the estuary revealed a stratified water column, perfectly divided during winter periods and the summer measurements (Figure 2.4). Water temperatures in the surface layer in winter and summer were about 10°C and about 30°C, and those from a depth of 2.5 m to the bottom were about 18°C and about 28°C in winter and summer respectively. Salinities in the surface layer were about 1-3, equivalent to freshwater, in the winter measurements and about 12, equivalent to brackish water, in the summer measurements. Salinities in the bottom layer from a depth of 3 m to the bottom were about 33-34 in both winter and summer. Thermocline and halocline were formed from depths of 1.5 m to 3 m in the winter. On the other hand, thermocline was from depths of 1 m to 1.5 m while halocline was from depths of 1.5 m to 2.5 m in summer.

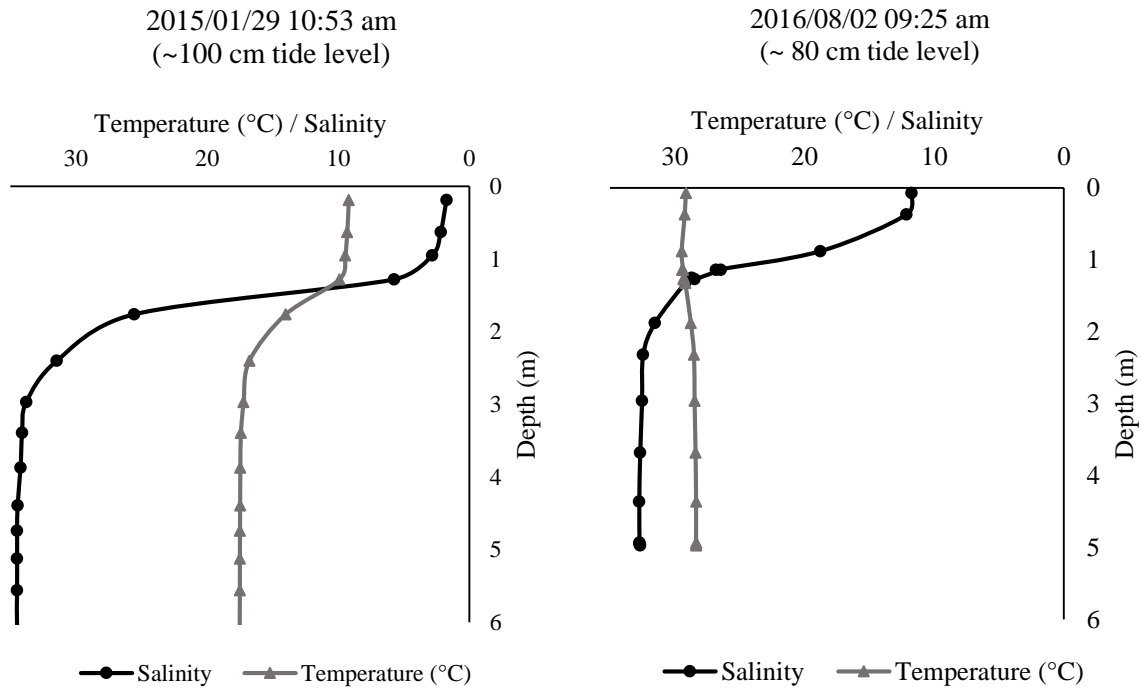


Figure 2.4 CTD measurements taken in an equivalent area of the main stream of Shimanto Estuary (see Figure 2.1) in January of 2015 (left) and August of 2016 (right).

Vertical profiles of salinity and water temperature in winter showed the stratification along the main stream of the estuary (Figure 2.5A), as well as along Ohshima Channel and Takeshima River (Figure 2.5B-C). Vertical profiles along the main stream of Shimanto Estuary showed that the upper limit of salt wedge was located at 6 km distant of the river mouth in winter of 2015 (Figure 2.4A) and nearly at the same place in summer of 2016 (Figure 2.6). Upper and lower estuary limits were located near the connection of main stream with Ushiro River in the upper reach of Shimanto Estuary, and at the estuary mouth in the lower reach, respectively.

This results are similar to the reports of Inouchi et al. (2006) on the incursion of the salt wedge in Shimanto Estuary and the vertical profiles of the main stream confirmed using echo sounders and CTD measurements. Using several measurements during winter and summer periods, Inouchi et al. (2006) found differences in the water level changes between summer and winter periods. However, the vertical profile of Shimanto Estuary was consistent and composed by a surface freshwater layer running and a bottom seawater layer separated by a brackish water mixing layer during the whole year. Thus, it is concluded that Shimanto Estuary can be classified as a highly stratified estuary (Dolan et al., 1972).

Seagrass beds were distributed in Takeshima River and Ohshima Channel in 2015-2016 as Kinoshita et al. (1988) reported in 1988. There was no attempt to confirm the presence of very small seagrass beds near shore areas of the main stream reported by Kinoshita et al., (1988). It seems nonetheless that the overall coverage of seagrass beds has been reduced in Shimanto Estuary in recent years (local reports, pers. observation), and might different to the reports of Kinoshita et al. (1988).

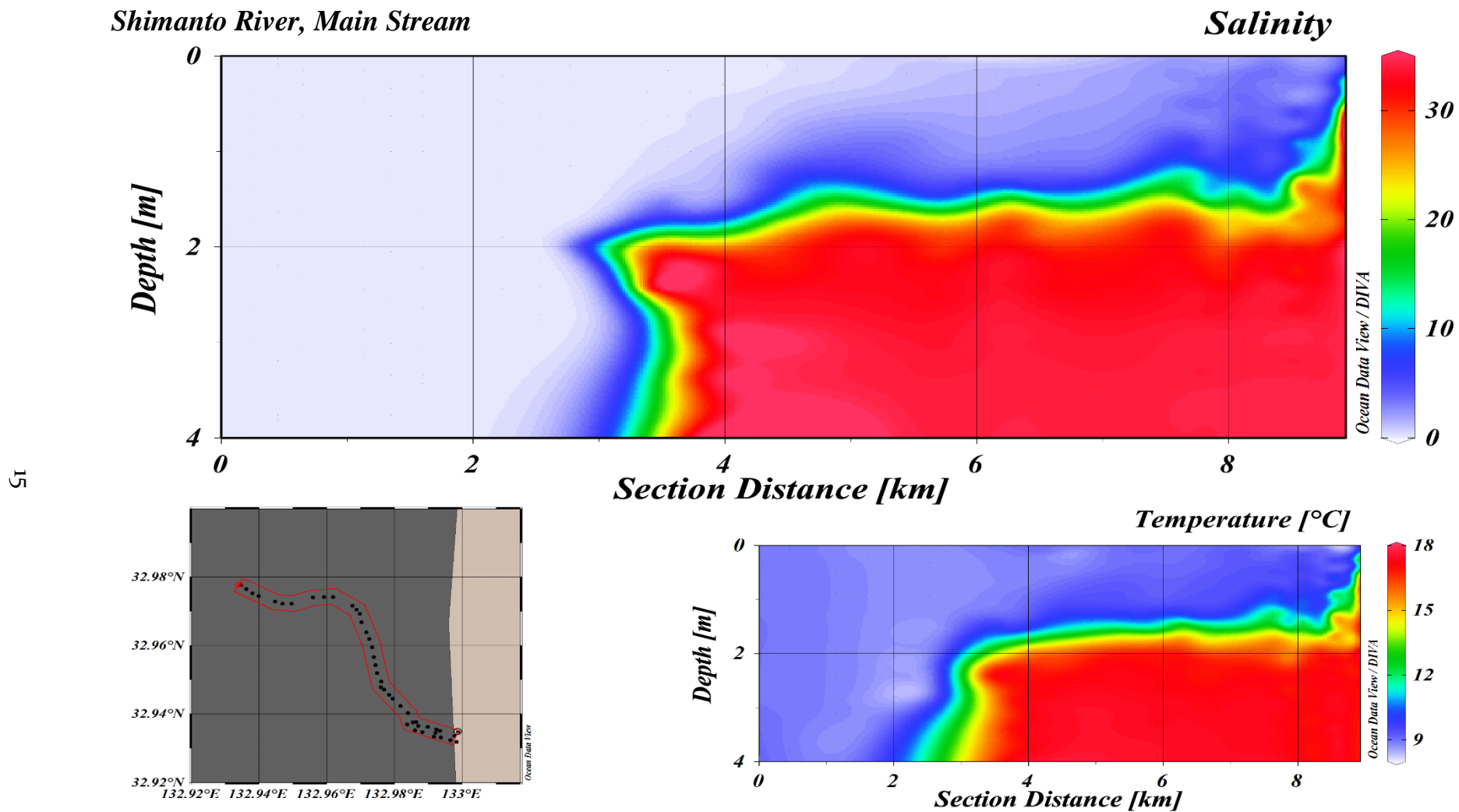


Figure 2.5 A Vertical profiles of salinity and water temperature in the first four meters of the water column along Shimanto River from 9 km upstream from the mouth to the river mouth based on the CTD measurements in January of 2015.

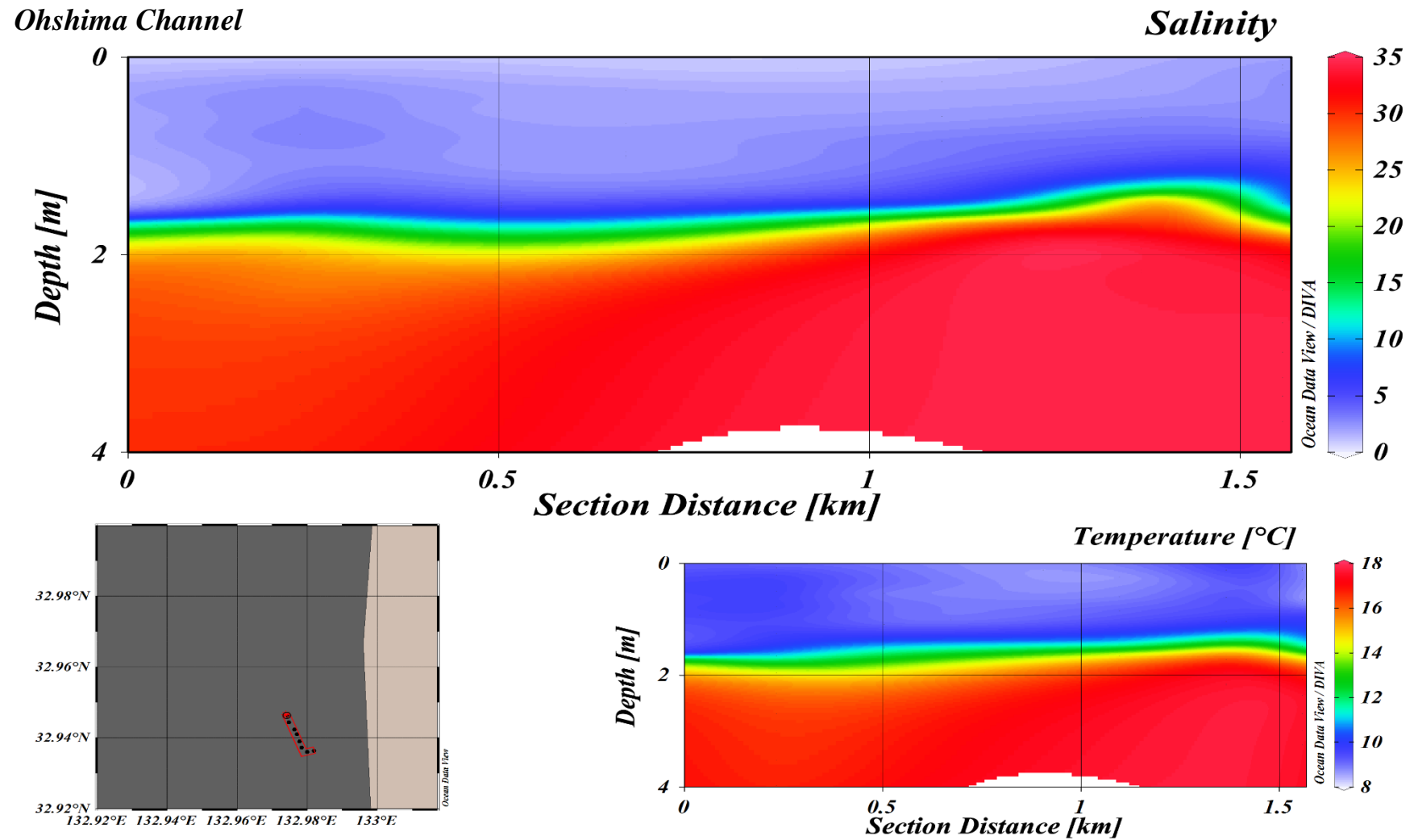


Figure 2.5 B Vertical profiles of salinity and water temperature in the first four meters of the water column along Ohshima Channel between its upper and lower confluence points based on the CTD measurements in January of 2015.

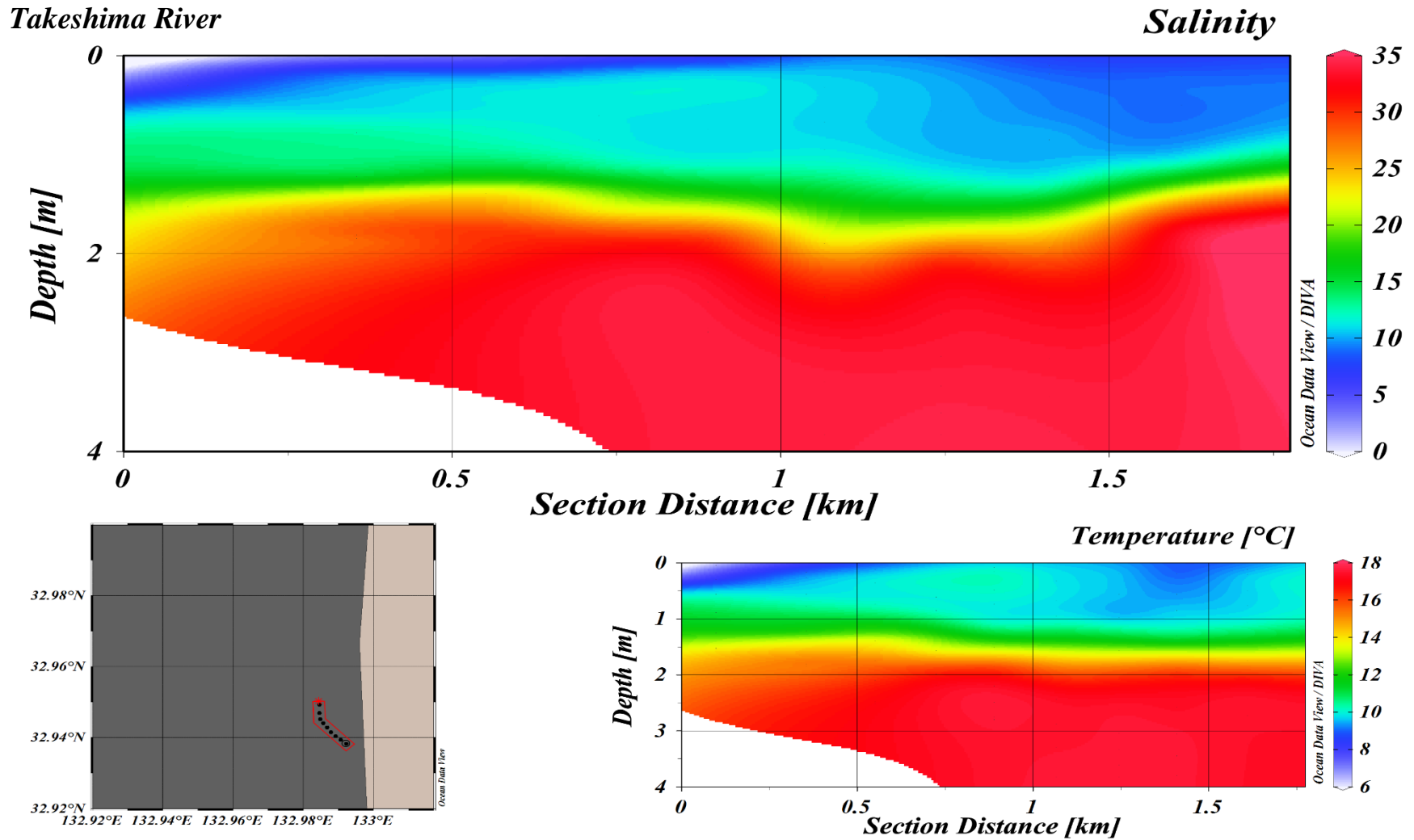


Figure 2.5 C Vertical profiles of salinity and water temperature in the first four meters of the water column along Takeshima River from 1.5 km upper from the confluence point to the confluence point based on the CTD measurements in January of 2015.

Shimanto River, Main Stream

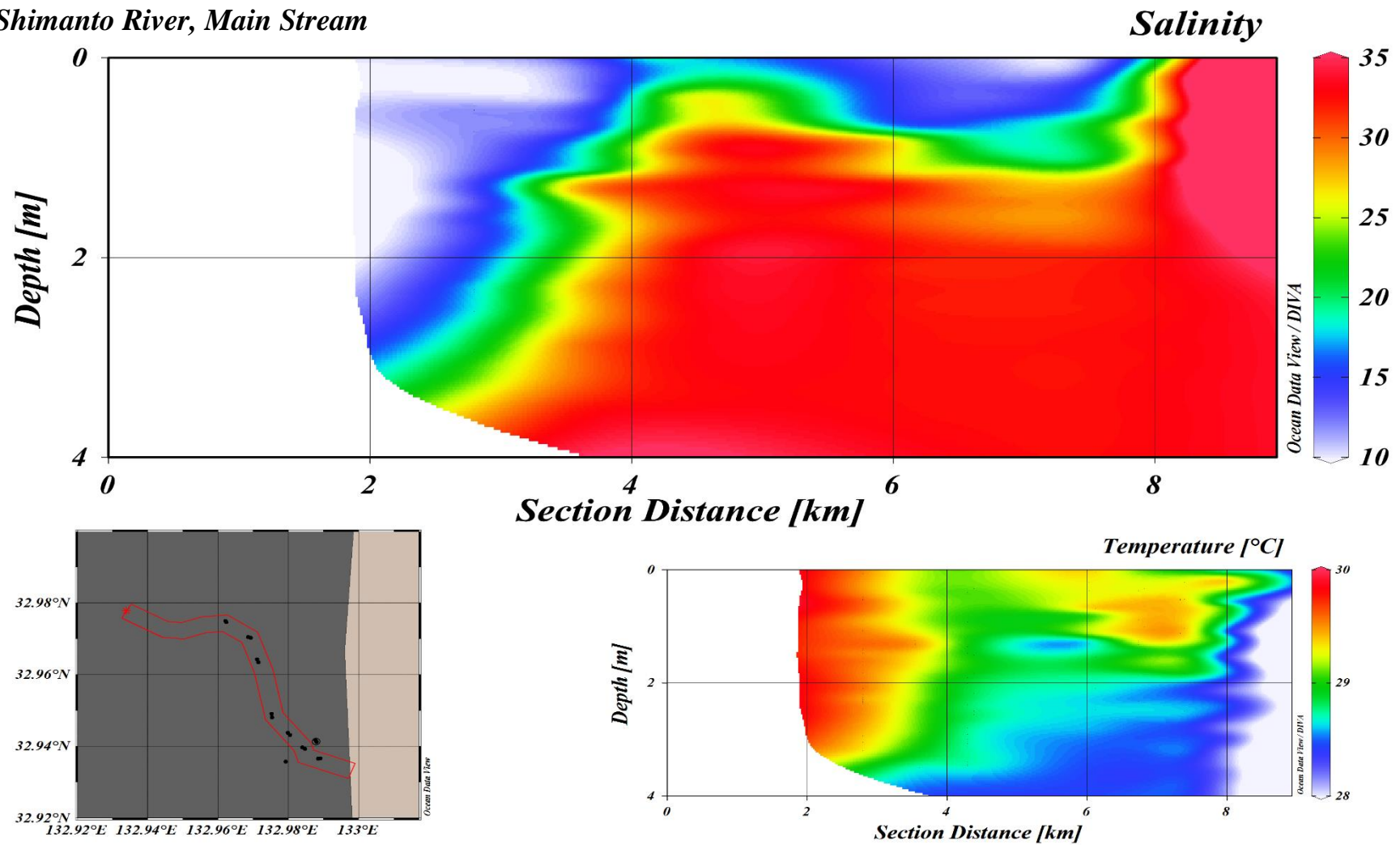


Figure 2.6 Vertical profiles of salinity and water temperature in the first four meters of the water column along Shimanto River from 9 km upstream from the mouth to the river mouth based on the CTD measurements in August of 2016.

Chapter III

Reconstruction of the life history of *Lates japonicus* in Shimanto Estuary with otoliths

**** The contents of pages 19 to 34 contain material intended for publication in an International Journal in the next 5 years, and are thus not available in this 2017 abridged version****

Chapter IV

*Habitat use of immature *Lates japonicus* during winter and spring released in Shimanto Estuary*

Introduction

Knowing the habitat use of immature *L. japonicus* in different time scales is important to be able to conserve them. One of the methods to study the habitat use of fish is acoustic biotelemetry. Acoustic biotelemetry systems, consisting of ultrasonic receivers fixed in arrays and acoustic transmitters attached to fish, are suitable for observing behaviors in temporal scales from hour to seasons. For a limited area like an estuary, a reduced number of acoustic receivers can fulfill the tracking necessities.

The Akame Gakuyukan is a local aquarium located in Shimanto City conducting activities for the promotion and conservation of the ichthyofauna of Shimanto Estuary, including that of *L. japonicus*. This facility had been independently conducting a program to foster juveniles of *L. japonicus* (<50 mm in total length) captured in seagrass beds in Shimanto Estuary until they reach immature stages (~400 mm in total length). Since mortality of juveniles are known to be higher than immature or mature individuals (Lorenzen, 1996), this program aims to enhance the survival rate during the juvenile period to increase the population of *L. japonicus* in Shimanto Estuary.

In general, it is very difficult to capture *L. japonicus* in the nature, moreover of specific body sizes. As the Akame Gakuyukan releases immature individuals in Shimanto Estuary, it is beneficial to use these individuals for tracking their behaviors in the estuary. Obtained results serve to investigate the habitat use of immature individuals as well as to evaluate the survival rate of immature individuals released in the nature after being reared in an aquarium from their juvenile period.

Materials and Methods

An acoustic transmitter (V9P-2H, Vemco Co.) was inserted in the peritoneal cavity of four immature *L. japonicus* of 42.5 ± 0.5 cm in total length (TL) and 1287.5 ± 43.8 g weight, donated by the Akame Gakuyukan. The V9P coded acoustic transmitter had a transmission delay of 200 – 400 s, with an expected battery life over 500 d, which greatly covered any seasonal period. The individuals were anesthetized by immersion in a tank with diluted clove oil (0.1 ml L^{-1}) for 15-20 min, and surgically implanted with the transmitter. After the surgery, each individual was immediately moved to its own tank to check its recovery. After a monitoring period of 24 h, all four individuals were healthy to release them in the estuary.

For observing their occurrences in temporal scales going from hours to seasons, acoustic receivers (VR2W, Vemco Co.) capable of detecting and the acoustic transmitters were set in fixed arrays in the estuary. These acoustic receivers can detect and identify the tagged individuals based on the acoustic signals emitted by the transmitters, when individuals enter the range where the acoustic receiver can capture the signals emitted by the transmitters.

In order to define the intervals to deploy the acoustic receivers in the estuary, the range where a receiver can capture acoustic signals from transmitters, known as the acoustic range (Pincock, 2008), was measured *in situ*. Different models of transmitters have different strengths of acoustic signals depending on their batteries and settings. To evaluate the particular acoustic range for the model that was attached to the immature *L. japonicus*, a range test was performed deploying six temporary arrays in the main stream of the estuary.

Temporally arrays were set at depths between 5 and 7 m, each one including a VR2W acoustic receiver (Vemco Co.), one V16 transmitter (Vemco Co.) and one V9P transmitter (Vemco Co.) attached to a thick rope. The rope was connected to a dead weight in one end and to a buoy in the other, keeping the receiver on a standing position in the water column (Figure 4.1). The receivers were set following the direction of the flow, separated 50 - 100 m from each other, comprising a total distance over 250 m between the both ends. Acoustic signal data from the transmitters were acquired with the deployed receivers during over three hours. Two-hour data acquired from one hour after the start of the experiment were analyzed to define the acoustic range of the transmitter.

The results of the range test indicated that a V9P model was efficiently (>80% accuracy) detected over 120 m in any direction, and probably over 200 m in good water conditions (>50% accuracy). These ranges are smaller than those presented in other studies using the similar transmitter models (e.g. Espinoza et al., 2011) because noises from currents might cover signals in the river or estuary. With this range, the width of most of the areas of the estuary can be covered with a single receiver if the acoustic receiver is positioned at the mid-point of the transversal section of the stream.

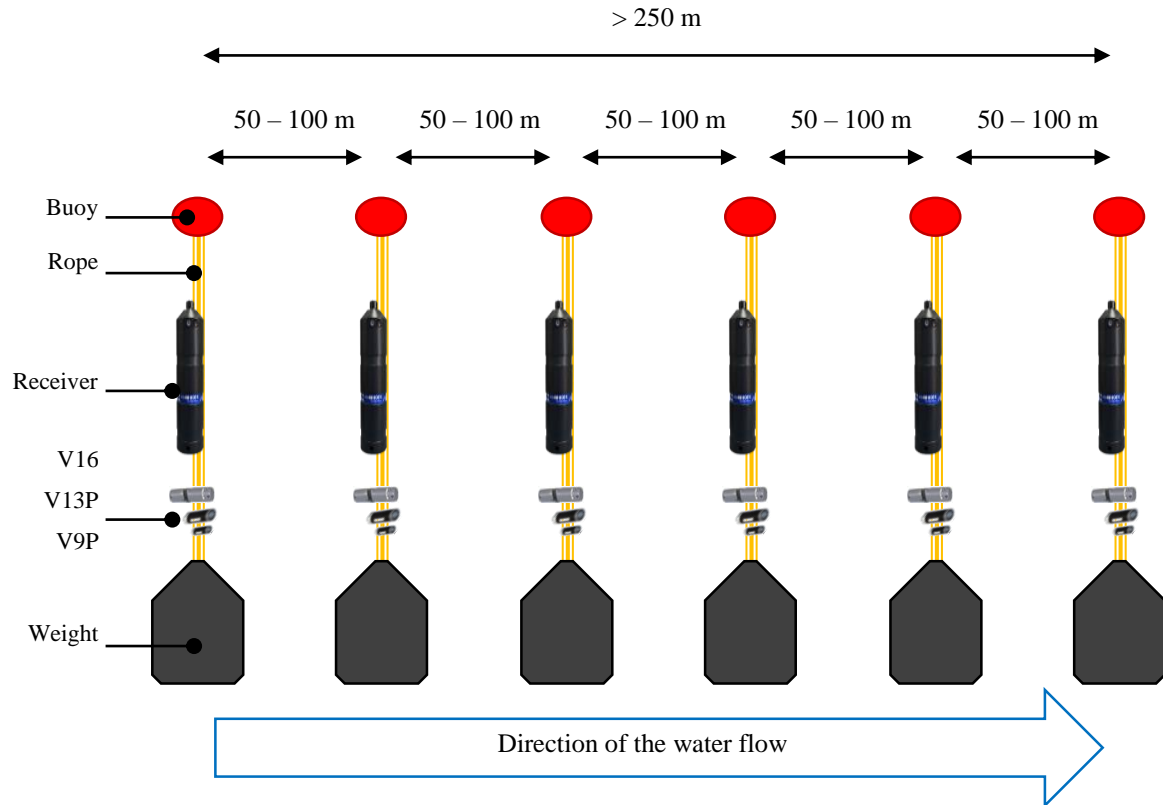


Figure 4.1. Schematic diagram showing the deployment of receivers along the main stream of the estuary for the estimation of the acoustic range between the receivers and the transmitters.

Before the tagged individuals were released one by one from the same point in the riverbank in the morning of October 23rd 2014 (Figure 4.2), acoustic receivers were deployed at a mid-point of the transversal section of the stream at depths of at least 4 m and up to 14 m. To prevent the loss of receivers, in the first deployment only two arrays were set in the estuary to confirm whether they weren't lost and they captured signals successfully, and four dummy settings were used to check other deployment areas.

The first deployment of two receiver stations (Stns.) and four dummy settings without acoustic tools was made on October 22nd 2014 prior to the release of individuals. The second deployment was made on February 24th 2015, after verifying that there was no loss of mooring receivers and dummy settings. Additional to the two stations set in October 22nd 2014, seven receivers were additionally deployed in lower part of the estuary (Figure 4.2). Seven receivers were set at Stns. A to G along the main stream of the estuary, one at Stn. H in lower end of Ohshima Channel, and one at Stn. I in Takeshima River.

From the nine deployed stations, eight stations (Stns. A to G and Stn. I) were retrieved at the planned date of June 8th 2015. One of the receivers (Stn. H) was recovered on March 15th 2016. All receivers had been working properly, and the stored data were successfully retrieved and analyzed. Data from the receivers was divided in three periods according to the number of stations that were deployed in the estuary.

The first period was defined from the release of the individuals on October 23rd 2014 to the second deployment of receivers on February 24th 2015, and the second period from February 25th 2015 to June 8th 2015. The receiver at Stn. H, that was recovered on March 15th 2016, had recorded acoustic signals from transmitters after June 8th 2015. These data were separately analyzed from those in the second period and named as the third period.

Detections were analyzed according to both the station where they were collected and the time that occurred. Notwithstanding differences among months and seasons, for convenience daytime was defined from 6 am to 5 pm at both periods, referring to the main average sunrise and sunset times during the tracking period, and the rest of the hours of the day assigned to night-time. Comparisons with the hourly tidal level were also made, using the data provided by the Japan Meteorological Agency on tidal levels in the area (www.data.jma.go.jp, data on KochiShimoda last accessed on October 24th 2016).

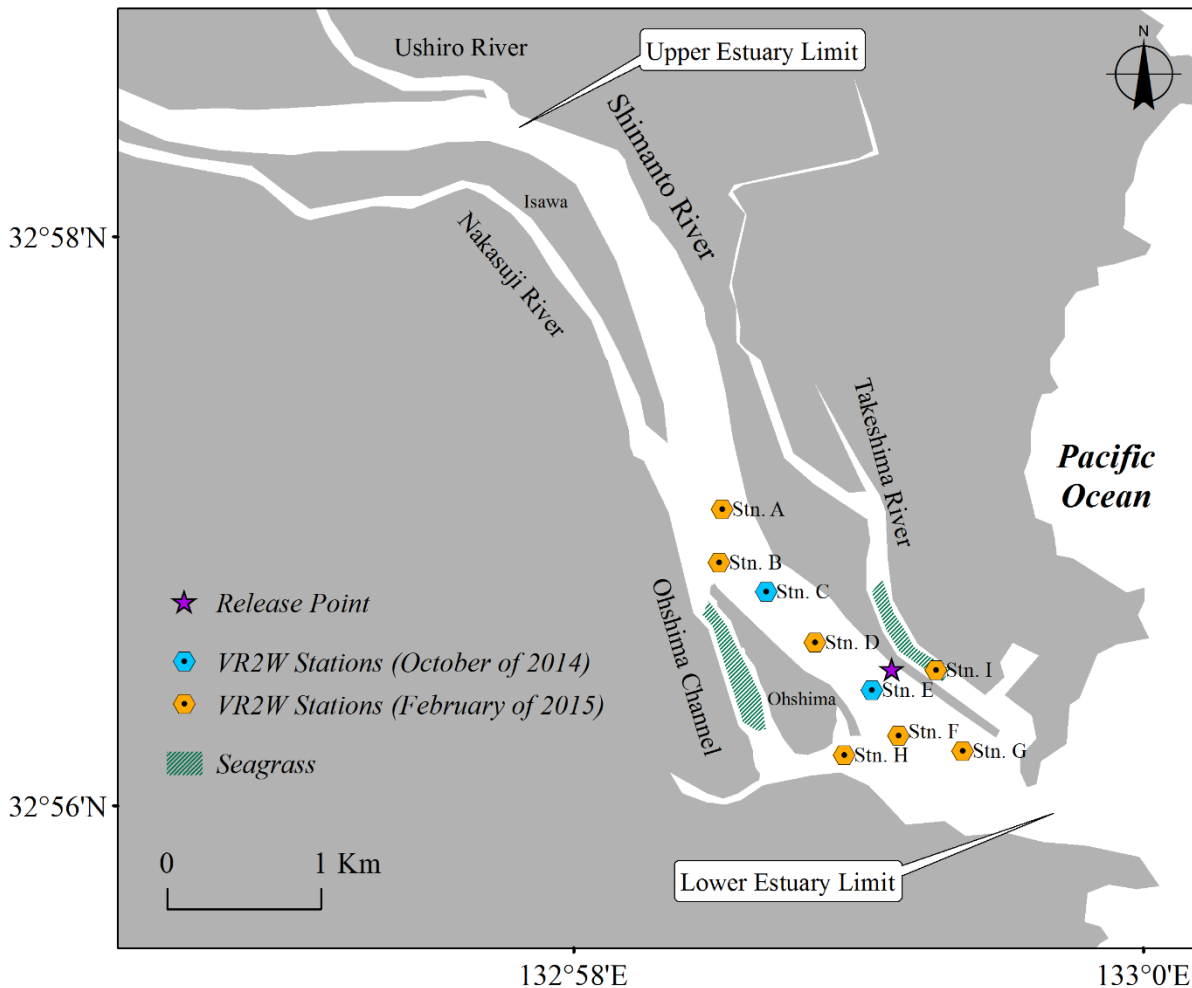


Figure 4.2. Map of Shimanto Estuary showing the points where the arrays containing VR2W acoustic receivers were deployed, and the release point of the tagged individuals. Shaded areas correspond to seagrass beds.

Results

After being released in the main stream, the four individuals moved to different directions. One individual, F1, was detected mainly in Takeshima River, while the other three, F2, F3 and F4, remained in the main stream of the estuary. The date of the last detection on each fish including detections in the third period at Stn. H was November 14th 2015 for F1 (387 days after release), June 12th 2015 for F2 (232 days after release), December 15th 2014 for F3 (53 days after release) and May 5th 2015 for F4 (194 days after release).

F1 was detected only 2 times at Stn. E during the first period. The first detection occurred during daytime immediately after being released in the main stream, and the second time occurred at night one month after in early December. During the second period, F1 was constantly and exclusively detected at Stn. I in Takeshima River. The 2447 detections of F1 at Stn. I occurred in the daytime (68.2%) with the day-peak of detections between 10 hr and 12 hr and at nighttime (31.8%), with the night-peak between 22 hr and 0 hr (Figure 4.3). Detections were often seen to occur during low or decreasing tides. After the second period, F1 was detected 7 times at St. H, especially at nighttime (85.7%), in late October and early November of 2015.

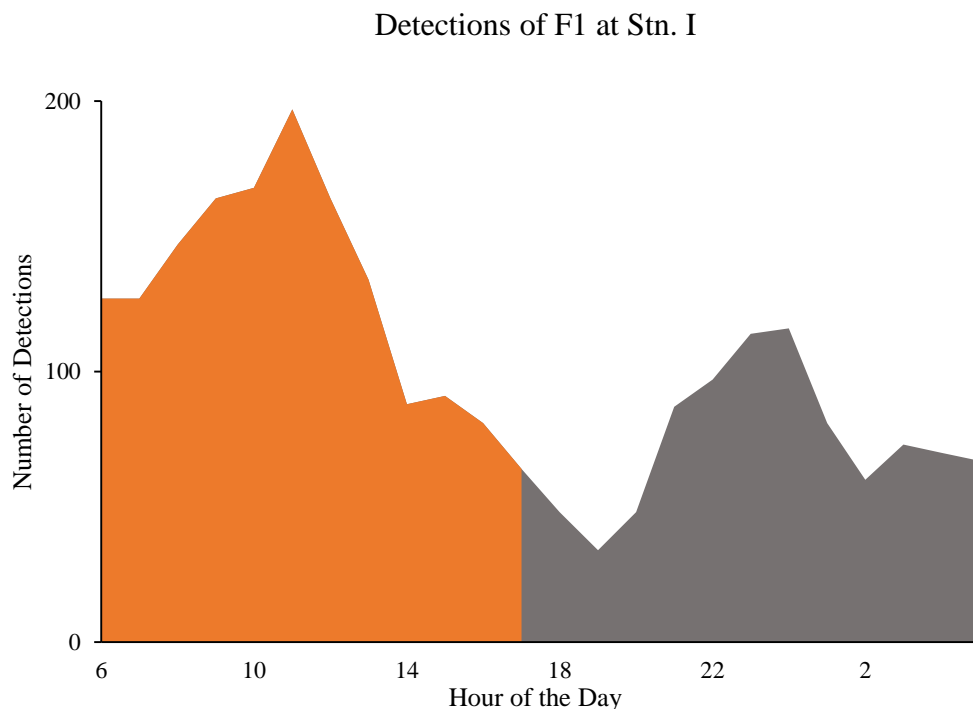


Figure 4.3. Detections of fish F1 at Stn. I in Takeshima River showing the frequency of detections according to the hour of the day during the second period of tracking. Detections in the daytime and at nighttime are colored in orange and grey, respectively.

F2 was infrequently detected with only 7 detections during the first period, 75 detections during the second period, and 3 detections at Stn. H during the third period. The 75 detections during the second period occurred at St. C (13 detections, 23.1% night-time) from early March to mid-April, and Stn. A in early March (62 detections, 76.9% night-time). F2 moved to the upper reaches of Ohshima Channel after released, and remained in Ohshima Channel from early March. During the third period, F2 was detected at Stn. H three times in June 2016 (100% night-time).

Individuals, F3 and F4, were frequently detected at Stns. C and E during the first period. F3 was detected 349 times consisting of 226 times at Stn. E (35% at nighttime) and 123 times at Stn. C (94.3% at nighttime). F4 was detected more frequently, a total of 1460 times, consisting of 711 times at Stn. E (51.9% at nighttime) and 749 times at Stn. C (99.7% at nighttime). It was observed that individuals F3 and F4 appeared at Stn. E during the daytime and nighttime (Figure 4.4 left). They appeared at Stn. C at nighttime from November 15th 2014 (Figure 4.4 right).

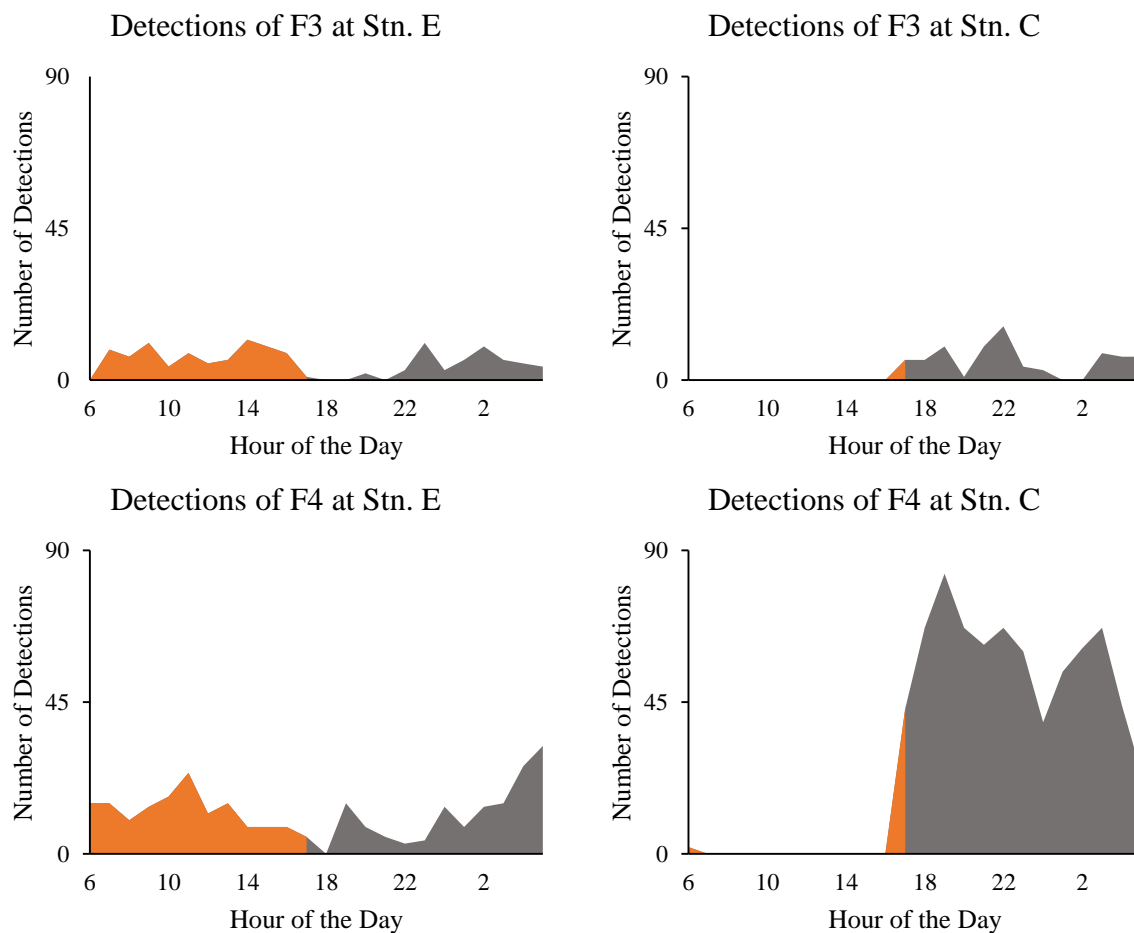


Figure 4.4. Detections of fish F3 and F4 at Stn. E and Stn. C during the first period between November 15th of 2014 and February 25th of 2015. Detections in the daytime and at nighttime are shaded in orange and grey, respectively.

During the second period, F3 was not detected in any of the stations, but F4 was detected a total of 2066 at Stns. A to E, consisting of 82.3% at nighttime. F4 was detected 1247 times (77.5% at nighttime) and 678 times at Stn. C (91.7% at nighttime). The increased number of detections in upper stream areas of the zone covered with acoustic receivers at nighttime (Figure 4.5) is related with a shift towards upstream residences. Night residences of F4 moved to areas near Stn. A and Stn. B from early spring in 2015, and day residences shifted from downstream areas of the main stream to an area outside the range of the receivers. The area might be located in Ohshima Channel.

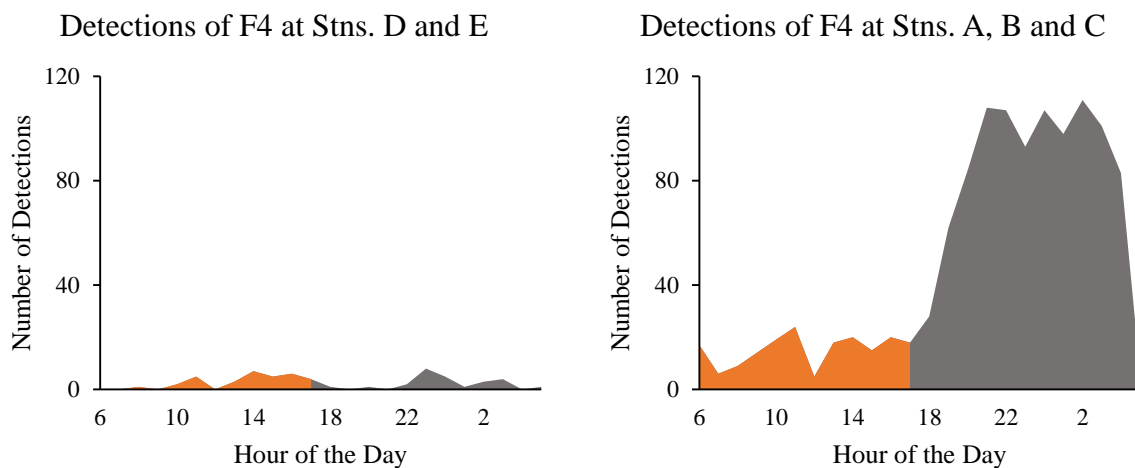


Figure 4.5. Detections of fish F4 during the second period of tracking grouped in downstream (left) and upstream (right) locations. Daytime detections are shaded in orange, nighttime detections in grey.

Discussion

The observed survival rates indicate that aquarium-reared forty-centimeters *L. japonicus* has low mortality inside the estuary. Except fish F3, which was only detected up to 53 days after release, all of the individuals were certainly alive for more than six months and inside estuarine waters. Survival for these extended period is indicative that individuals were properly adapting to the estuarine habitats and that had assured a food supply to subsist.

No detection of any fish occurred at the two downstream locations, Stn. F and Stn. G, indicating that likely none of the individuals moved towards the sea. All individuals presented a clear affinity for estuarine waters never showing any particular interest in moving towards coastal areas. Inside the estuary, the seagrass areas located in Takeshima River and Ohshima Channel were of the most frequented and the places where all tracked individuals concentrated.

Temperature, salinity and depth conditions in Ohshima Channel and Takeshima River are similar to each other. These areas are characterized by small streams, shallow water depths and bottoms covered with seagrass beds as described in Chapter II. The seagrass beds of Ohshima Channel are a reported hot-spot for larvae and small juveniles of *L. japonicus* in Shimanto (Kinoshita et al., 1988). The acoustic detection records suggest that these areas might be a preferred habitat for late juvenile stages of *L. japonicus* too. It seems that conditions on these streams are suitable not only for small juveniles, but also for immature *L. japonicus* at forty-centimeters size.

The receiver in Takeshima River was located in deeper waters in the lower end of the seagrass bed area. It is speculated that during high tides F1 moved to the shallower upper stream areas where seagrass is abundant, and during low tides returned to deeper waters near the receiver. The day-night shifts between areas for F3 and F4 might indicate the need for more than one habitat. During winter, both day and night residences were located at different areas in the main stream. From early spring, night residences moved upstream to the upper connection of Ohshima Channel with the main stream, and day residences were likely located in the channel. This tendency of occurrences suggests that seagrass beds were favored during the daytime, while the main stream was preferred as a night habitat.

At sizes over 20 cm TL, *L. japonicus* is thought to feed mainly on fish (Uchida, 2005), using a powerful sucking action (Tanoue et al., 2012) to ingest the whole prey at once. For a forty-centimeters *L. japonicus*, preferable preys will probably be small fish, often abundant near or in seagrass beds. The prey availability in the seagrass beds located in Takeshima River and Ohshima Channel can be a main cause for the observed occurrences.

The seagrass beds are very important for juveniles and immature individuals of *L. japonicus* in Shimanto Estuary. *L. japonicus* is thought to leave seagrass nurseries a little after the first winter of their life is over, when individuals measure near 12 cm TL (Uchida, 2005). However, it seems that juveniles and immature individuals might be linked to estuarine seagrasses much longer than previously thought. The results of the tracking also showed a steady stay in the estuarine habitats, since individuals never displayed any particular interest in moving towards coastal areas nor passing upper boundary of Shimanto Estuary.

Seagrass beds in the estuary are limited to two narrow areas. It is possible that the carrying capacity of seagrass beds limits the number of juveniles and immature individuals. More research is necessary on the carrying capacity of these habitats to estimate the maximum number of individuals per year that could be released without having a negative impact on wild populations of *L. japonicus* in Shimanto Estuary. Seagrass beds of *Z. japonica* are decreasing in most coastal and estuarine environments in Japan. The reduction of *Z. japonica* beds can negatively impact the population numbers of *L. japonicus*, and therefore it is necessary to monitor and control the evolution of these important habitats in Shimanto Estuary.

Chapter V

Movements of wild Lates japonicus during the spawning season

**** The contents of pages 43 to 53 contain material intended for publication in an International Journal in the next 5 years, and are thus not available in this 2017 abridged version****

Chapter VI

Habitat use and behavior of *Lates japonicus* revealed with a digital still-camera logger

Introduction

Improvements of digital imaging systems gives new opportunities to study fish behaviors (Delcourt et al., 2013). Animal-borne cameras can observe behaviors of free-ranging animals at a fine-scale (Davis et al. 1999, Watanabe et al. 2003; Mitani et al., 2004; Moll et al., 2007), and have successfully been used to study the behavior of several marine species (e.g. Ponganis et al., 2000; Fuiman et al., 2002). Combination of a digital imaging system with data-loggers that can measure several ambient parameters permits to understand the animal's environment while studying behavior.

Incorporation of new and improved sensors to animal-borne cameras has resulted in a new generation of devices that can be used to study complex behaviors of aquatic animals in relation with ambient conditions (Naito, 2006; Naito, 2007). The digital still-camera logger (DSL) has been used for studying behaviors of aquatic animals in relation with their environment (e.g. Kudo et al., 2007; Watanabe et al., 2008). Methods of deployment and recovery of animal-borne data-logger systems, including the DSL, have been developed (Watanabe et al., 2008).

In order to investigate the habitat use of adults of *L. japonicus* into more detail, the data recorded with an animal-borne digital still-camera logger (DSL) attached to wild-caught big *L. japonicus* in 2009 was analyzed. Analysis of obtained images and environmental data could provide critical knowledge on the habitat use and behavior of *L. japonicus* in Shimanto Estuary.

Materials and Methods

A digital still-camera logger (Little Leonardo Ltd., 22×133 mm, 82 g in air) was attached to wild *L. japonicus* with a total length of 89 cm and a weight of 9.4 kg captured in Shimanto Estuary with line and a lure, hereafter called as the experimental individual. Its size suggested that it had already reached adult stages as it was over 60 cm TL (Uchida, 2005), but its sex wasn't checked to avoid increasing handling time and stress.

A small rubber net was sutured in front of the dorsal fin of the experimental individual with dissolvable silk sutures. A floater with the DSL, a VHF transmitter (Advanced Telemetry Systems, Inc.), an acoustic transmitter (V13P, Vemco Co., 13 × 44 mm, 12 g in air) and a 3-axis acceleration logger (ORI-380D3GT, Little Leonardo Ltd., 12 × 45 mm, 8 g in air) was fixed to the rubber net on the experimental individual using a time-release explosive bridle (Figure 6.1) to detach the package (Watanabe et al., 2008). The package was adjusted for neutrally buoyancy before attachment to the fish. The experimental individual equipped with the animal-borne package including the DSL was released in upper areas of Shimanto Estuary (Figure 6.2) at 06:00 on July 14th 2009 by a research team lead by Dr. Hideaki Tanoue.

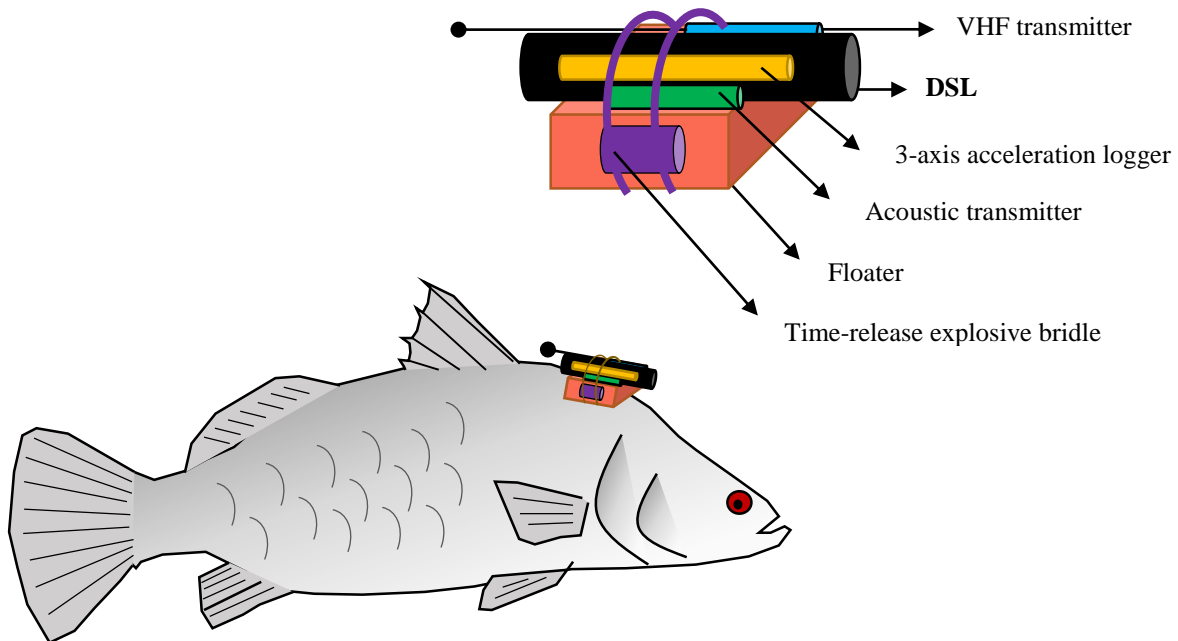


Figure 6.1. Schematic view of a *Lates japonicus* equipped with the floater system consisting of a Digital Still-camera Logger, an acoustic transmitter, a VHF radio transmitter and a 3-axis acceleration logger via a time-release explosive bridle.

The position of the individual after its release was tracked by acoustic signals emitted by the V13P acoustic transmitter with a VR100 (Vemco Co., Canada) lowered from a boat and a GPS. The floater system was automatically detached from the fish by the time-release explosive bridle at 11:00 on July 14th 2009. The position of the floater system in the surface after detachment was searched with the aid of a radio antennas and a receiver system (Advanced Telemetry Systems, Inc.) to track the radio signals emitted by the VHF transmitter.

The DSL took a total of 4563 images at intervals of 4 s during 5 h and 7 min from the release to the detachment of the floater system from the fish. Image data from the DSL was downloaded to a computer after recovery of the floater system and kept stored. Information on depth and water temperature recorded by the 3-axis data-logger were linked to images taken by the DSL with time recorded on the images.

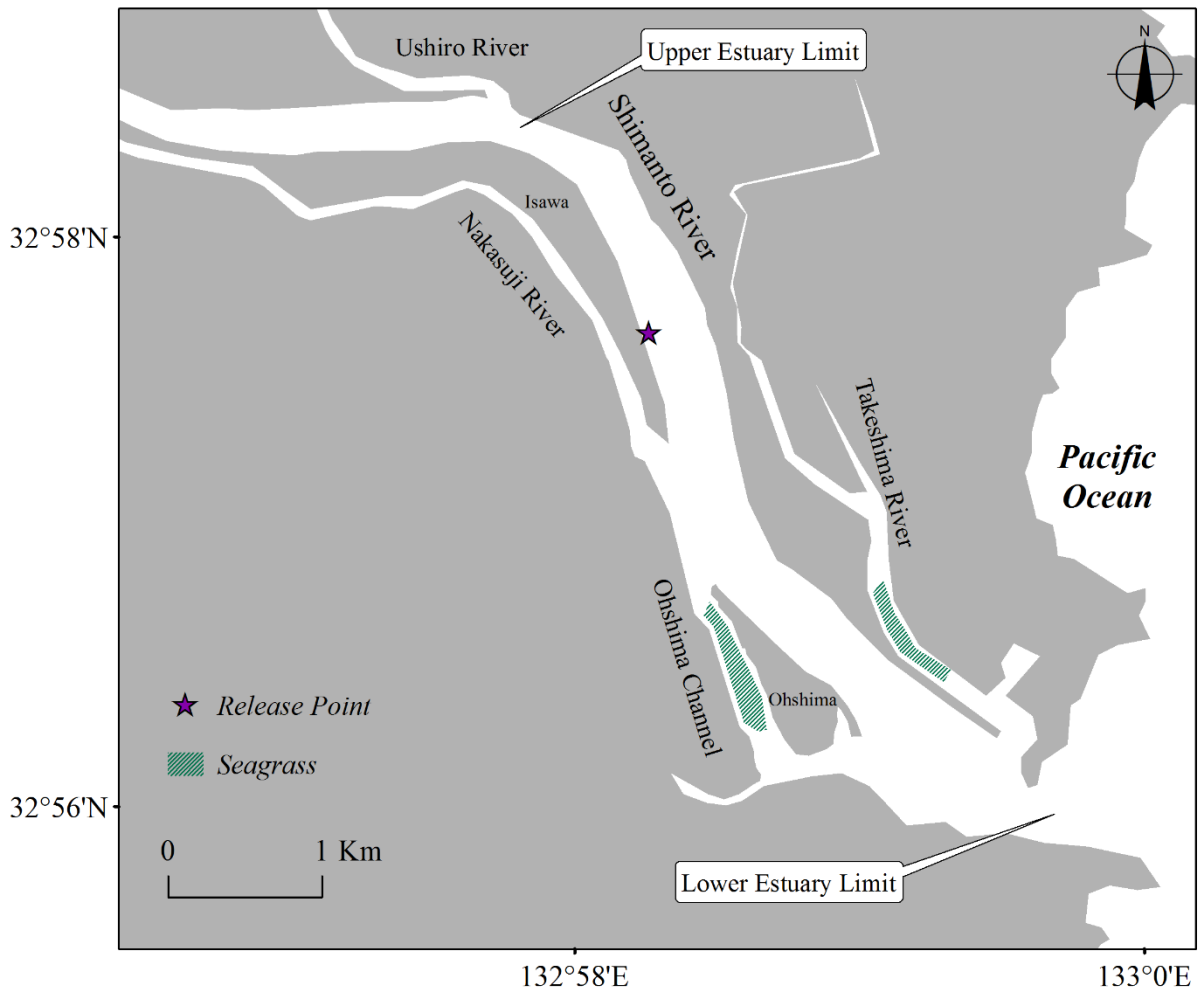


Figure 6.2. Map showing Shimanto Estuary, the release point of the *Lates japonicus* equipped with the floater system including the digital still-camera logger (star mark). Shaded green areas correspond to seagrass beds.

The images obtained by the DSL were analyzed individually and classified according to their contents. At the first step, the images were classified into those that include some fish or didn't include any fish species. At the next step, the images containing fish were divided in two categories, those including *L. japonicus*, and those of any other fish species. At the third step, all images were also classified into images with bottom substrates or only water column. The former images were classified into bottom substrates (e.g. rock, sand, gravel) according to the definition of river beds by Wolman (1954).

Results

During the entire duration of the experiment, the experimental individual remained close to the release point, in deeper areas of the estuary. The recorded depth ranged between 1.0 m and 7.9 m, with a mean of 3.9 ± 1.8 m. The mean recorded water temperature was 28.4 ± 0.5 °C, with a minimum of 24.5 °C and a maximum of 28.7 °C.

Among the 4563 pictures collected, the types of bottom observed were sand (62%) and gravel (34%). Only 496 images (10.8%) contained fish on them, and 472 of those (95.2%) included at least part of the body of a *L. japonicus*. Inside the 24 images of other fish species (Figure 6.3), 12 corresponded to sharpnose tigerfish (*Rhynchopelates oxyrhynchus*), 7 to yellowfin seabream (*Acanthopagrus latus*), and 5 to flathead grey mullet (*Mugil cephalus*).



Figure 6.3. Two images on fish from the animal-borne still-camera logger: (left) several sharpnose tigerfish (*Rhynchopelates oxyrhynchus*) and (right) a yellowfin seabream (*Acanthopagrus latus*).

Of all the images not including fish, 1248 images comprised some particular structures or fishing tools. A formation of large rocks appeared in 830 images, and one of two types of fishing gears did in 418 images (Figure 6.4). Among the images including one of the two fishing gears, 188 images were bottle traps and that of 230 images were brushwood traps. Several images on fishing gears were taken on the same fishing gear of bottle or brushwood trap.



Figure 6.4. Two types of fishing gears captured with the animal-borne digital still-camera: a brushwood trap (left), and a bottle trap (right).

A total of 472 images included *L. japonicus* (Figure 6.5) with a mean recorded depth of 2.9 ± 0.4 m, and an average water temperature of 24.9 ± 0.02 °C. The average number of individuals captured together in the same image was 1.4 ± 0.7 , with a maximum number of 4 individuals at the same time. Other *L. japonicus* first appeared in the images over 4 h after the release of the individual, 31.5 min before the detachment. Groups of *L. japonicus* were found at both of the observed types of bottoms, slightly predominating the images taken at sandy areas. In some of the images including plural *L. japonicus*, a perfectly aligned configuration of *L. japonicus* was observed, but in the others, they were more randomly positioned.

Diving profiles of the experimental individual recorded with the 3-axis acceleration showed that the experimental individual dived rapidly to deeper layer of the river with depths more than 7 m, where the 71 images taken were black because of no enough light for taking images. After the deep diving, it returned to shallower layer with depths of around 2 m, where it remained for more than 2 h. Then, it stayed in an intermediate depth of around 4 m until the end of the recording. The water temperature increased in deeper areas and decreased at the surface, because the bottom layers were occupied with warm seawater covering the bottom and the surface layers with cooler low salinity water derived from the river. Analysis of the 3-axis accelerations obtained with the logger indicated no potential feeding event, judged from the criteria for *L. japonicus* established by Tanoue et al. (2012).

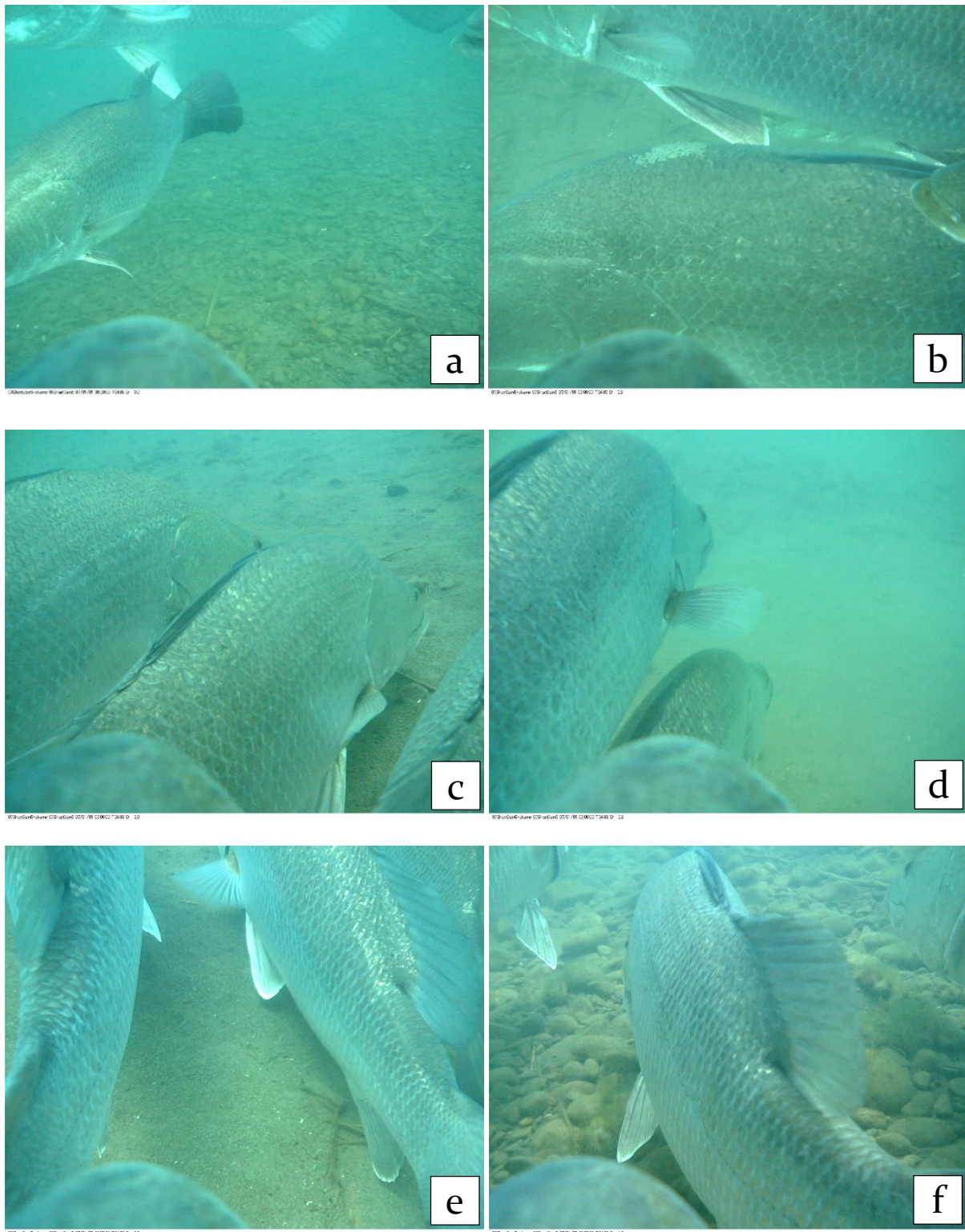


Figure 6.5. Images showing groups of *Lates japonicus* in different organization styles. Image (a) showed a swarm consisting of individuals swimming to different directions and (b) a group swimming in a different position to the experimental individual. Images (c-e) showed a school consisting of polarized individuals swimming organized with the released fish.

Discussion

The images revealed that *L. japonicus* likely spends most of its time swimming close to the bottom. Observed bottoms corresponded to both gravel and sandy, likely located in areas near the incursion of the salt wedge according to the recorded depth and tracking. Although the depths during the experiment widely changed, groups were observed at depths near 4 m. In upper stream areas, depths near 4 m or over are found in the areas towards the middle of the stream. It is possible that adults of *L. japonicus* prefer habitats located at intermediate depths (~4 m) in upper areas of the estuary.

Several individuals of this species were observed swimming close to other congeners (Figure 6.5). These images revealed for the first time that *L. japonicus* forms shoals (Pitcher, 1983; Pitcher, 1986) of schools or swarms (Delcour & Poncin, 2012) in Shimanto Estuary in summer. The shoals consisted of relatively similar big-sized individuals probably similar to the size of the released fish, which can be related to adult sizes and maybe to individuals belonging to the same age-class that often are blood related (Frommen et al., 2007). The observed size of fish is thought to have virtually no predator inside Shimanto Estuary to cause a response of remaining together for protection, or being confined to a specific area of the estuary. Shoals are unlikely to provide any feeding benefits in a *L. japonicus* of the observed size and it can even reduce the amount of prey obtained (Bertram, 1978).

The benefits obtained from shoaling in fish have been discussed for a long time, especially in regards to motivations that lead shoals to occur (Shaw, 1978; Partridge, 1982). One of the possible motivations for this behavior of *L. japonicas* may be reproduction. This study was carried in July during spawning season of the species estimated from late June to early August (Kinoshita et al., 1988; Iwatsuki et al., 1994). In the results of the acoustic tracking of wild adults (Chapter V), adult *L. japonicus* remained in the upper reaches of the estuary. And the DSL showed that in the upper reaches of the estuary, adult *L. japonicus* formed the shoals. It is possible for adult *L. japonicus* prepare the spawning behavior with formation of shoals in the upper reaches.

In the few hours of recording, fishing tools were observed, showing the possible interaction of human activities with *L. japonicus* in the estuary even when is only targeted by sport fishermen. *L. japonicus* is known to be a “strong fish”, able to survive capture and transport (Tashiro & Iwatsuki, 1995), and catch-and-release is known to have low mortality rates (Alós et al., 2009; Veiga et al., 2011). Under certain restrictions to ensure that released fish survive with minimum stress, and avoid captures at sensitive periods such as spawning times, catch-and-release activities can be compatible with protection objectives. A balance between conservation measures and sustainable angling can be achieved to ensure the continuity of this fish in Shimanto Estuary, whilst allowing sport anglers to continue enjoying this remarkable species.

Chapter VII

General discussion

**** The contents of pages 61 to 64 contain material intended for publication in an International Journal in the next 5 years, and are thus not available in this 2017 abridged version****

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