

Isotopic evidence of connectivity between an inshore vegetated lagoon (nursery habitat) and coastal artificial reefs (adult habitats) for the reef fish *Lethrinus lentjan* on the Terengganu coast, Malaysia

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Abstract. Stable isotope analyses of muscle tissue ($\delta^{13}\text{C}_{\text{muscle}}$ and $\delta^{15}\text{N}_{\text{muscle}}$) and otoliths ($\delta^{13}\text{C}_{\text{otolith}}$ and $\delta^{18}\text{O}_{\text{otolith}}$) were used to retrospectively track habitat uses of *Lethrinus lentjan*, and to determine any association between Setiu Lagoon (nursery habitat) and coastal artificial reefs (CARs; adult habitats) on the Terengganu coast, Malaysia. Muscle stable isotopes exhibited a spatial change from inshore to offshore habitats associated with growth, possibly related to the reef-ward movement of the fish. Otolith stable isotopes of adult fish from CARs were measured in juvenile (from outside the core to the first opaque zone of otolith) and adult (the edge of otolith) portions and were compared with those of juveniles from Setiu Lagoon, suggesting that the adult fish may not primarily use the lagoon as a nursery before ontogenetically migrating to CARs. The effects of coastal currents between monsoonal seasons could reorientate offshore juvenile migration; hence, adult cohorts in CARs may be replenished from various nursery habitats along the coast. Additionally, similarities in the $\delta^{18}\text{O}_{\text{otolith}}$ values of juvenile and adult sections suggested that some individuals may not spend their juvenile phases in shallow estuarine habitats. Based on the findings of this study, we recommend that coastal conservation strategies take into account multiple nursery habitats rather than a single one.

Additional keywords: ecological linkage, muscle, otolith, stable isotopes.

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Introduction

Coral reefs are an important habitat for numerous commercially important target species, reef fisheries providing an important source of protein and livelihood for coastal human communities (Rioja-Nieto and Alvarez-Filip 2019). However, over- and destructive fishing, coastal development and pollution have threatened coral reefs in many tropical regions, including the east coast of Peninsular Malaysia (ECPM; Burke *et al.* 2012). The rapid degradation of coral reefs has resulted in a reduction of fisheries products, particularly high-value commercial reef fishes (Cruz-Trinidad *et al.* 2014). However, an increase in available coastal shelters close to nursery habitats can potentially increase recruitment to a fishery and therefore aid in fisheries recovery (Rilov and Benayahu 2000; Arney *et al.* 2017).

The surrogate shelters provided by coastal artificial reefs (CARs) are considered to provide important habitats for post-settlement fish and other benthic reef macrofauna (Bohnsack 1989; Dupont 2008; Arney *et al.* 2017). In addition, adult populations on CARs can be replenished from adjacent natural coral reefs as ‘spillover’ effects of protected marine areas (Carr *et al.* 2017). Accordingly, CARs have been installed off the Terengganu coast as a conservation technique to increase and enhance the abundance of fishes and fish stock, fisheries management, aquaculture, research and recreation (Jensen 2002; Seaman 2007; Ali *et al.* 2013; Cresson *et al.* 2014). Some reef fishes, such as snappers, groupers and emperors, are generally recognised as migrating with growth from juvenile nursery areas, such as seagrass meadows and mangroves in estuaries, to adult habitats on reefs

(Nagelkerken *et al.* 2002; Mumby 2006; Luo *et al.* 2009; Honda *et al.* 2013; Kimirei *et al.* 2013a). Nevertheless, limited information is available regarding the fish sources supplying such reefs, or the link between reef fish nursery and CAR habitats, despite the crucial importance of such information for the design of optimal fish management strategies for sustainable use and conservation.

The pink ear emperor fish (*Lethrinus lentjan*) is a very important commercial species for marine fisheries in subtropical and tropical regions of the Indian and Indo-Pacific oceans, including Malaysian coastal waters (Carpenter *et al.* 2016). However, this high-value species has been heavily exploited and possibly overfished in and around coral reefs (Carpenter *et al.* 2016). Being a reef-associated species, *L. lentjan* occurs in various habitats throughout its lifespan, including mangroves and seagrasses as juveniles before ontogenetically migrating to coral reefs as adults (Kimirei *et al.* 2013a, 2013b; Carpenter *et al.* 2016; Le *et al.* 2018). A previous study reported that juveniles (41–150-mm total length, TL) prefer to inhabit the mangrove–seagrass continua rather than the mangroves without adjacent seagrasses in Setiu Lagoon because mangroves are often exposed during low tide (Le *et al.* 2018). Furthermore, during our primary surveys conducted in mangrove estuaries, such as Kuala Besut, Sungai Keluang Besar, Sungai Semaarak, Merang Terengganu and Sungai Ibai, along the Terengganu coast in 2015, only a limited number of juveniles was found. Unlike juveniles, high densities of adult cohorts (>160 mm TL) were recorded from coral reefs and CARs off Terengganu coastal waters (Ali *et al.* 2013). Even though size-distributed populations related to resource utilisation abilities and predation risk support an ontogenetic habitat shift in reef fish species from estuarine and marine areas (Werner and Gilliam 1984; Nakamura *et al.* 2008), evidence of population connectivity is still lacking. Hence, this raised the possibility that Setiu Lagoon may be one of several important nursery habitats that replenish adult *L. lentjan* in the CARs along the Terengganu coast.

Resolution of the possible role of Setiu Lagoon was deemed most likely from stable isotope analyses of fish muscle tissue and otoliths due to the difficulty of tracking movements of individual fish between aquatic habitats using conventional methods, such as mark and recapture, biologging and genetic population structure analysis (Amano *et al.* 2015). Mark and recapture and biologging methods are limited by recapture rates, marking procedures, fish size dependence and technical demands, whereas genetic approaches are limited by the dynamic nature of oceanography and the often subtle genetic structures resulting from large effective population sizes and high potential for larval dispersal (Amano *et al.* 2015).

Stable isotope analyses of fish muscle tissues have been widely used to determine dietary sources, feeding habits and trophic levels (Post 2002; Vaslet *et al.* 2011; Reis-Santos *et al.* 2015; Davis *et al.* 2015; Abrantes *et al.* 2015). Whereas stable carbon isotope ($\delta^{13}\text{C}$) signatures in fish tissues can reflect corresponding isotope signatures of local vegetation-based food webs in which the fish has grown (photosynthetic pathways of C_3 v. C_4 plants; Fry and Sherr 1984; Abrantes *et al.* 2015), the degree of enrichment of stable nitrogen isotopes ($\delta^{15}\text{N}$) can be used to estimate the trophic level of fish in the food web (Post 2002). Isotope compositions in fish muscle tissues often reflect

time-integrated values of food sources and habitat utilities, the turnover times of the former in tissues varying from weeks to 6 months, allowing the tracking of fish movements or ontogenetic diet changes over short periods during growth (Tieszen *et al.* 1983; Herzka 2005; Fry 2008; Nakamura *et al.* 2008). Conversely, during the formation of new otolith material throughout the life of a fish, elements and isotopes in ambient waters are incorporated permanently into the carbonate matrix in a layered manner (Campana 1999; Campana and Thorrold 2001; Elsdon *et al.* 2010), thereby preserving the timing of deposition, which can be used as a proxy to provide a detailed history of the fish's environment (Brazner *et al.* 2004; Kimirei *et al.* 2013b), ontogenetic migration (Huxham *et al.* 2007; Reis-Santos *et al.* 2015), dietary sources (Elsdon *et al.* 2010) and stock discrimination (Edmonds *et al.* 1999; Bastow *et al.* 2002; Gao *et al.* 2005; Amano *et al.* 2015). Owing to trophic interactions and ontogenetic niche shifts frequently being size dependent, differences in individual fish sizes are commonly observed within populations (Werner and Gilliam 1984). Gradual changes in the isotope composition of fish tissues associated with size classes (growth) may reflect the mixture of a new diet and habitats because the fish are new arrivals, hence inferring population connectivity, if there is clear isotope discrimination between inhabited environments (Nakamura *et al.* 2008; Vaslet *et al.* 2011; Le *et al.* 2018). Indeed, during ontogenetic offshore migration, reef fishes may move across vegetated nursery estuaries as juveniles (shallow, low saline, warmer water) to adult habitats on coastal reefs (deep, high saline, cooler water). Discrete isotope incorporation in otoliths can reflect environmental changes (Elsdon *et al.* 2008). In recent years, an increasing number of studies has used otolith $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ as markers to retrospectively identify fish migration, rather than trace elements, because reef fishes usually inhabit environments with uniform water chemistry (Campana 1999; Mateo *et al.* 2010; Kimirei *et al.* 2013b; Amano *et al.* 2015). In fact, stable oxygen isotopes in otoliths ($\delta^{18}\text{O}_{\text{otolith}}$) are deposited in, or very near to, isotopic equilibrium with ambient waters (Radtko *et al.* 1996; Campana 1999; Elsdon and Gillanders 2002; Huxham *et al.* 2007; Kitagawa *et al.* 2013). Using $\delta^{18}\text{O}_{\text{otolith}}$, Weidman and Millner (2000) found a significant correlation between $\delta^{18}\text{O}_{\text{otolith}}$ and ambient water temperature at the time of aragonite formation in the otolith. Conversely, Bowen (2010) found spatial variations in oxygen stable isotopes associated with salinity changes in oceanic surface waters, because they both arose from sea surface processes such as evaporation–precipitation, continental run-off, upwelling–advection and melting–freezing (Delaygue *et al.* 2001; McConnell *et al.* 2009). Accordingly, Shirai *et al.* (2018) used $\delta^{18}\text{O}_{\text{otolith}}$ to reconstruct the salinities experienced by fishes in a mangrove estuary in Urauchi Bay, temperature not being considered because of the narrow variations of water temperature in subtropical and tropical regions. Thus, $\delta^{18}\text{O}_{\text{otolith}}$ can be used reliably to reconstruct salinity experiences in subtropical and tropical fishes, if the fish move across a spatial salinity gradient (Shirai *et al.* 2018). Unlike oxygen, stable carbon isotope in otoliths ($\delta^{13}\text{C}_{\text{otolith}}$) is more complex, because the carbon sources incorporated may include the diet (Nelson *et al.* 2011), dissolved inorganic carbon (DIC) in ambient waters taken up via the gills and intestinal interfaces (Kalish 1991;

Nelson *et al.* 2011) and metabolic effects (Kalish 1991; Weidman and Millner 2000; Trueman *et al.* 2016). Such factors may result in incorrect interpretation of fish migration history. However, in some cases $\delta^{13}\text{C}_{\text{otolith}}$ may be useful for tracking fish movement if the spatial pattern of isotope signals from the fish environment shows a steep gradient or is strong enough for discrimination between sources of variability (Schwarcz *et al.* 1998; Mateo *et al.* 2010; Kimirei *et al.* 2013b).

The aim of the present study was to retrospectively track the nursery habitat use of adult *L. lentjan* collected from CARs, using muscle ($\delta^{13}\text{C}_{\text{muscle}}$ and $\delta^{15}\text{N}_{\text{muscle}}$) and cross-sectioned otolith ($\delta^{13}\text{C}_{\text{otolith}}$ and $\delta^{18}\text{O}_{\text{otolith}}$) stable isotope analyses. Specifically, the aim of the study was to determine whether fish had developed in the Setiu Lagoon (nursery habitat) before migrating to CARs along the Terengganu coast. Comparisons of stable isotopes in post-larval (juvenile) and margin (adult) otolith portions of adult fish with those in surface otoliths of juvenile fish collected from the lagoon should indicate whether the adult *L. lentjan* had originated from the Setiu Lagoon nursery. To improve the reliability of different environment determinations, reef (i.e. fully marine) and freshwater fishes were used to establish end-member habitat values as reference points.

Materials and methods

Typical regional monsoonal climates

The ECPM, located in the southern South China Sea, is continuous with the Gulf of Thailand and Vietnam coast to the north and north-east respectively. The region has an annual tropical monsoon climate that controls surface circulation along the coast. The North-east Monsoon (NEM; from October to March) brings greater rainfall compared with the South-west Monsoon (SWM; from April to September), April and October representing transitions between the two monsoons (Akhir 2012; Akhir *et al.* 2014). Sea circulation, driven by monsoon wind seasons, affects the reef environments along the coast. During the SWM, coastal currents flow northward along the ECPM and advect water masses from the Java Sea (Qu *et al.* 2005), in association with strong upwelling from Kuantan coast, bringing cool salty water along the coast (Daryabor *et al.* 2015; Kok *et al.* 2015). Accordingly, sea surface temperatures and salinity along the Terengganu coast range from 28.6 to 29.0°C and from 32.1 to 32.6 practical salinity units (PSU; Akhir *et al.* 2014). During the NEM, surface current eddies advect water southward from coastal Vietnam, there being an absence of coastal upwelling. Temperature and salinity in the study area ranged from 29.2 to 30.9°C and from 31.5 to 31.8 PSU (Akhir *et al.* 2014; Daryabor *et al.* 2015). Unlike the two main monsoon seasons, slow currents are usually observed during the short inter-monsoon periods (Akhir *et al.* 2014; Daryabor *et al.* 2015; Kok *et al.* 2015).

Study sites

The study was conducted to examine ecological connectivity between an inshore area (i.e. the shallow brackish water Setiu Lagoon) and an offshore area (i.e. CARs along the Terengganu coast, ECPM; Fig. 1). The Setiu Lagoon, ~14 km long and 300–800 m wide (Fig. 1), is considered a potential nursery habitat for various commercial fishes, particularly *L. lentjan*, due to its habitat configuration, hydrology and mosaic

vegetation habitat (Le *et al.* 2018). The mangrove forests are dominated by *Rhizophora* spp., *Avicennia* spp. and *Nypa* spp. *Halodule pinifolia*, the dominant seagrass species with a mean canopy height of 18 cm, forms meadows or small patches near the *Rhizophora* mangrove forests or close to the mouths of the lagoon. The lagoon is subjected to semidiurnal tides (tidal range 1.7 m), water depth varying from 0.2 to 2 m above the seagrass beds at low and high tides. Water flow and exchange in the lagoon were driven by tidal regimes through two open inlets during the sampling period. Previous surveys indicated somewhat uniform salinity within the seagrass areas (fluctuating between 25 and 28 PSU) during the SWM (dry season) due to very low precipitation, and stratified salinity during the NEM (wet season), decreasing to 5 PSU in surface water at peak rainfall, but steady at ~18–24 PSU in the bottom layer (Le *et al.* 2018). The water temperature varied slightly between the seasons, ranging between 28 and 32°C.

The CARs (the offshore study area) have been deployed by the Department of Fisheries Malaysia since 1975, being attractive habitats for various reef fish species, including snappers, emperors, groupers and trevally. In addition, the artificial reefs provide hard surfaces where corals, algae and oysters attach (Ali *et al.* 2013). Owing to adult *L. lentjan* having been identified as an offshore resident (Lugendo *et al.* 2005; Carpenter *et al.* 2016), the CARs are considered to provide adult habitat for the species. The target CARs, constructed from reinforced concrete, included cuboid (size 2.0 × 2.0 × 3.0 m; weight 10 Mg module⁻¹) and cube forms (size 2.5 × 2.5 × 2.5 m, weight 16 Mg module⁻¹), which were deployed at a depth of 15–20 m over an area of ~125 × 50 m (Ali *et al.* 2013).

Sampling

Pink ear emperor fish *L. lentjan* were collected in the Setiu Lagoon as juveniles and from offshore CARs along the Terengganu coast as adults (Fig. 1). All juvenile samples from the Setiu Lagoon were collected using gill nets during ebb tides in both 2016 and 2017. The 10 samples from 2016 (size 9–14.5 cm TL, and subject of a previous study; Le *et al.* 2018), included 5 specimens collected in January (corresponding to NEM) and 5 collected in July (corresponding to SWM; Site 1). In 2017, five juvenile samples were collected in July at a second site (Site 2) in the lagoon to verify spatial and interannual variations in otolith isotope composition, but no juveniles were collected in January (Fig. 1). Following Carpenter *et al.* (2016), all the juveniles were considered as young-of-the-year or of age 1 year. Based on previous surveys in Le *et al.* (2018), the juveniles were found only in seagrass beds adjacent to mangroves (salinity 20–28 PSU) and at no time were found in low-salinity areas in the lagoon or freshwater area of the input river basin; hence, the species likely occurs within a certain salinity range (Le *et al.* 2018).

In all, 23 adult pink emperor fishes of various body size were collected from CARs ~10–12 km off the Terengganu coast. Of the adult samples, 18 were purchased from local fishermen using cage traps at the CARs in April 2016 (corresponding to post-NEM; 11 specimens) and August 2016 (7 specimens), and 5 were speared by divers using SCUBA in August 2016 (corresponding to SWM). All adult samples were confirmed as being caught in the studied CARs by fishermen, although several other CARs, surrounding Bidong and Redang, were

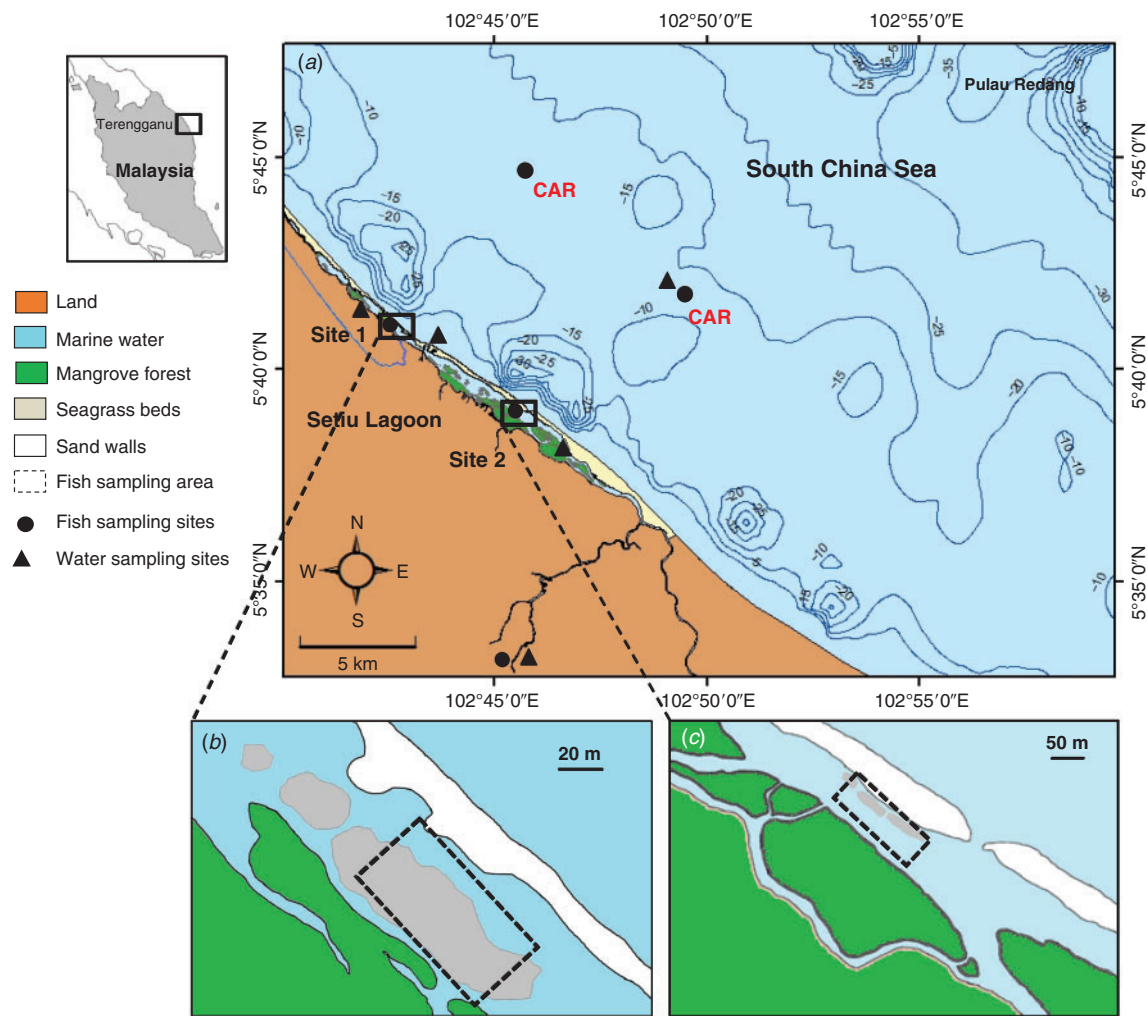


Fig. 1. Sampling areas. (a) Setiu Lagoon and coastal artificial reefs (CARs) off Terengganu coast. (b) The seasonal sampling site in 2016 (Site 1). (c) The sampling site in July 2017 (Site 2).

~20 km from the study site. Natural coral reefs also surround islands off the Terengganu coast, including Cipu, Lang Tengah, Perhentian, Bidong and Redang; Perhentian and Redang islands are included in marine protected areas (MPAs) of the Marine Park Malaysia.

To establish end-member habitat values, adult fish from freshwater and marine habitats were collected following Shirai *et al.* (2018). The adult freshwater fish included *Trichogaster pectoralis* (two specimens), *Barbonymus schwanenfeldii* (two specimens) and *Channa micropeltes* (two specimens), purchased from a local market upstream in the Setiu River, whereas the adult marine fish included *Caesio cuning* (three specimens), *Chlorurus japanesis* (three specimens) and *Lutjanus vitta* (five specimens), collected from a single CAR in August 2016. For an environmental history reference of fishes in the lagoon, samples of the brackish-water resident *Apogon hyalosoma* (five specimens) were collected for otolith stable isotope analyses.

To determine whether any ontogenetic dietary or habitat shift occurred from inshore to offshore areas, various potential food items were sampled from the lagoon and CAR habitats.

According to Carpenter *et al.* (2016) and Le *et al.* (2018), *L. lentjan* is a demersal carnivore, taking primarily crustaceans, molluscs, echinoderms, polychaetes and small fishes. Juvenile *L. lentjan* prefer crustaceans, polychaetes and molluscs (Le *et al.* 2018), whereas adults target crustaceans, molluscs and echinoderms (Toor 1964; Carpenter *et al.* 2016). Lagoon food items were used as described by Le *et al.* (2018), whereas food items from CARs, including small sea cucumbers (*Holothuria* spp.; six specimens), molluscs (Pinnidae; four specimens) and annelid worms (two specimens), were collected by divers using SCUBA in August 2016.

All fish samples were packed in labelled polyethylene bags and immediately stored in coolers, transported to the laboratory and frozen at -20°C until further processing.

Ambient water temperature and salinity were measured using a YSI multiparameter meter (ProPlus, Yellow Springs, OH, USA), before water samples were collected for oxygen stable isotope analysis along a salinity gradient from upstream in the Setiu River to the Setiu Lagoon to the offshore CARs. The vertical distributions of salinity and temperature in the water column at

the CARs were taken from *Akhir et al. (2014)*, who reported interannual variability from the surface to a depth of 30 m of 28.5–30.9°C in temperature and 31.5–33.3 PSU in salinity.

Water samples for determination of the salinity gradient were taken from the CARs (33 PSU), at three points along the salinity gradient (31, 21.8 and 9 PSU) in the lagoon and in fresh water (0 PSU) upstream in the Setiu river during the ebb tide in August 2017 (Fig. 1) and kept in clean 20-mL glass vials in a cool box. The water samples collected in triplicate from each sampling site were preserved at 5°C and transported to the Atmosphere and Ocean Research Institute, The University of Tokyo, for further analysis.

Sample preparation and stable isotope analysis

The TL (to the nearest millimetre) and bodyweight (to the nearest gram) of fish samples were recorded, and dorsal white muscle tissue was taken for stable isotope analyses. All tissue samples were dried at 60°C for 24 h before grinding into fine powder with a mortar and pestle. Sagittal otoliths were extracted from each fish, and the length and width measured using callipers (to an accuracy of 0.01 mm) before being cleaned with deionized water. The otoliths of adult *L. lentjan* from CARs were large enough (length 7.3–15.4 mm, width 5.5–13.3 mm) for microdrilling through different life stages. Random juvenile and adult otoliths were selected for analysis, there being no significant differences in stable isotopes between the left and right sides (*Campana 1999; Huxham et al. 2007*).

Tissue samples

Stable isotope ($\delta^{13}\text{C}_{\text{muscle}}$ and $\delta^{15}\text{N}_{\text{muscle}}$) compositions of the tissue samples and potential food items were measured using a stable isotope ratio mass spectrometer (IsoPrime100; IsoPrime, Cheadle, UK) coupled with a combustion device (vario MICRO cube; Elementar, Langenselbold, Germany) at the Atmosphere and Ocean Research Institute, The University of Tokyo, as described by *Le et al. (2018)*. Data for juvenile *L. lentjan* collected from the lagoon were taken from *Le et al. (2018)*.

Otolith samples

Selected otoliths were ground with a graded series of alumina paste to expose the core along the anterior–posterior axis after being embedded in epoxy resin (Araldite Rapid R30, Nichiban Co., Ltd, Tokyo, Japan) on a glass slide. After polishing, the otoliths were cleaned with Milli-Q water and dried. Based on alternating growth increments and light reflection under a microscope, three otolith zones in large adults (18 specimens; >220 mm TL) were identified as representing larval, post-larval and adult periods (*Blacker 1974; Schwarcz et al. 1998; Fig. 2*). However, the adult period in otoliths of small adult fish (three specimens; 154–184 mm TL) were either unclear or seen as narrow zones beyond the post-larval period. The larval period was identified as a dark spot in the centre of the otolith (core), and the post-larval period (juvenile portions) was defined as a region of rapid growth apparent as the first opaque zone of the otolith, determined within an interval of ~350–850 μm from the core depending on otolith size and shape. These intervals were considered as representing the first year of life, corresponding to a body size of juvenile fish (6–15 cm TL) collected from the

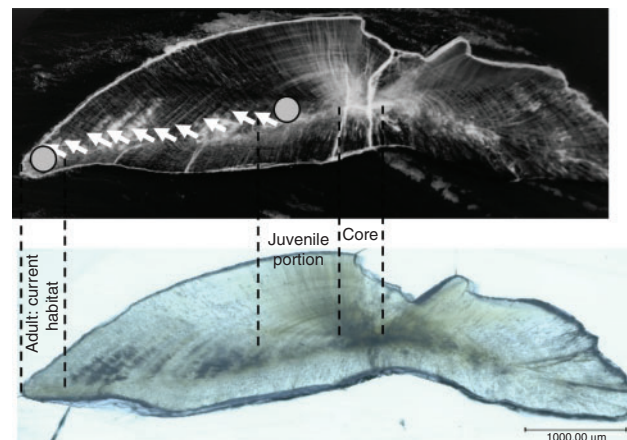


Fig. 2. Identification of otolith zones based on light reflection. Arrows indicate growth increments. Three main zones were identified in the adult otolith: the core (central dark spot), the post-larval period (juvenile; region of fast growth between the core and the first arrow) and the adult period (likely inhabiting coastal artificial reefs; marginal portion indicated by the last arrow). The circles indicate drilling positions.

lagoon and noted in an earlier study (*Kimirei et al. 2013a*). The otolith margin, beyond the post-larval interval region with a regular series of alternating growth bands called translucent and opaque zones, was considered as the adult period (hereafter ‘adult portion’), likely reflecting recent habitats. Otolith margins were analysed for *L. lentjan* juveniles (hereafter ‘juveniles’) and the end-member fish species. A triangular pyramid drilling bit of a high-precision micromilling system with accurate positioning on a 1/1000-mm scale (GEOMILL326; Izumo-web Ltd., Izumo, Shimane, Japan) was used for post-larval and adult portions in the same individual, two cone-shaped drilling samples (diameter 250 μm , depth 250 μm) being taken from each portion on the same side of the otolith. After milling, the otolith powder was collected onto aluminium foil and transferred to a glass vial for isotope analysis. The otolith was photographed using a digital microscope (VHX-5000; KEYENCE, Itasca, IL, USA) before and after each micromilling exercise to confirm the portions.

Analyses of otolith stable isotopes of carbon ($\delta^{13}\text{C}_{\text{otolith}}$) and oxygen ($\delta^{18}\text{O}_{\text{otolith}}$) were conducted at the Atmosphere and Ocean Research Institute, The University of Tokyo. The powder sample was measured using an isotope ratio mass spectrometer (Delta V plus; ThermoFisher Scientific, Waltham, MA, USA), equipped with an automated carbonate reaction device (GasBench II; Thermo Fisher Scientific). Otolith powder was introduced into a glass vial, flushed with pure helium and reacted with 100% phosphoric acid at 72°C. Liberated CO_2 was transported with the helium gas flow to the mass spectrometer. Detailed analytical conditions have been reported elsewhere (e.g. *Kubota et al. 2017; Shirai et al. 2018*). All isotope values are reported using delta notation with respect to Pee Dee Belemnite (PDB), based on an NBS-19 (International Atomic Energy Agency, Vienna, Austria) value of -2.20‰ for $\delta^{18}\text{O}_{\text{otolith}}$ and $+1.95\text{‰}$ for $\delta^{13}\text{C}_{\text{otolith}}$. No correction was applied to the acid fractionation factor between calcite and aragonite (phosphoric acid–calcium carbonate reaction temperature 72°C; *Kim et al. 2007a*). Repeated analysis of the NBS 19 standard yielded an

Table 1. Otolith stable isotope values in different habitat residents as end-member patterns and referenceData are given as the mean \pm s.d. Stages are based on FishBase (<https://www.fishbase.in/search.php>, accessed 31 May 2019). TL, total length

Fish type	Species	Otolith		Muscle		TL (cm)	Stage
		$\delta^{13}\text{C}$ (‰)	$\delta^{18}\text{O}$ (‰)	$\delta^{15}\text{N}$ (‰)	$\delta^{13}\text{C}$ (‰)		
Freshwater residents (end-member)	<i>Barbonymus schwanenfeldii</i>	-16.3 ± 0.5	-6.4 ± 0.4	7.0 ± 0.8	-25.1 ± 0.5	20.7 ± 0.8	Adult
	<i>Trichogaster pectoralis</i>	-11.9 ± 0.8	-7.0 ± 0.4	11.7	-28.6	17.2 ± 0.6	Adult
	<i>Channa micropeltes</i>	-19.4 ± 0.6	-6.5 ± 0.8	3.6 ± 0.4	-24.5 ± 0.3	34.7 ± 6.1	Adult
Marine residents (end-member)	<i>Caesio cuning</i>	-7.4 ± 0.7	-2.3 ± 0.1	9.3 ± 0.2	-17.9 ± 0.2	29.2 ± 2.1	Adult
	<i>Chlorurus japanesis</i>	-6.9 ± 0.9	-2.3 ± 0.2	8.1 ± 0.3	-17.5 ± 0.0	30.8 ± 4.7	Adult
	<i>Lutjanus vitta</i>	-4.3 ± 0.6	-2.2 ± 0.1	10.9 ± 0.4	-16.1 ± 0.5	22.4 ± 1.3	Adult
Brackish-water residents (reference)	<i>Apogon hyalosoma</i>	-7.5 ± 1.2	-3.6 ± 0.6	10.1 ± 0.4	-20.5 ± 0.9	13.9 ± 0.7	Adult

external reproducibility of $\delta^{18}\text{O}_{\text{otolith}}$ and $\delta^{13}\text{C}_{\text{otolith}}$ measurements better than 0.14 and 0.13‰ respectively (1σ).

Water samples

Oxygen isotope compositions of the water samples ($\delta^{18}\text{O}_{\text{water}}$) were determined using a Picarro L2130-i Analyzer (Picarro, Inc., Santa Clara, CA, USA) at the National Institute of Technology, Ibaraki College. Before introduction to the analyzer, samples were filtered using a membrane filter (pore size 0.45 μm ; Toyo Roshi Kaisha, Tokyo, Japan) to reduce suspended particles and avoid blocking the sampling line. Samples were analysed and mean values are presented, the deviations being smaller than long-term reproducibility. Data are reported in delta notation against the Vienna Standard Mean Ocean Water (VSMOW) reference standard. Long-term instrument reproducibility was $\pm 0.02\text{‰}$.

Statistical analysis

Values are expressed as the mean \pm s.d. Prior to analysis, all stable isotope data were tested for normality using the Shapiro–Wilk and Levene's tests. If the data did not fit a normal distribution, non-parametric tests were conducted. Student's *t*-test was used to test the significance of differences in the stable isotopic signatures between freshwater and seawater fishes. Mahalanobis distances were used to detect outliers, which were then removed before further tests (Barnett and Lewis 1994). Relationships in this study were examined using linear regressions. To examine a specific nursery and past habitat use of fish in the study areas, multivariate analysis of variance (MANOVA) was conducted to test whether otolith stable isotope signatures of juveniles from the lagoon and the juvenile portions of adult fishes from CARs were distinguishable from each other with regard to different sampling periods (seasons). If adult fish exhibit otolith stable isotope (OSI) areas in juvenile portions similar to those in juveniles, they could be considered to have occupied similar nursery environments. In contrast, different isotope ratio values indicate either different nursery environments experienced during the juvenile phases or that the lagoon is not the only nursery habitat supplying the adult habitat. Mean $\delta^{13}\text{C}_{\text{otolith}}$ and $\delta^{18}\text{O}_{\text{otolith}}$ values for juvenile *L. lentjan* and otolith portions of adults were compared using one-way analysis of variance (ANOVA) or Kruskal–Wallis tests. A one-sided significance level of $\alpha < 0.05$ was used in all

tests. Statistical analyses, including identification of outliers, were performed using SPSS Statistics for Windows (ver. 25, IBM Corp., Armonk, NY, USA). Graphs were drawn using R (ver. 3.2.4, see <https://cran.r-project.org/>, accessed 11 June 2019) and SigmaPlot for Windows (ver. 11, Systat Software, San Jose, CA, USA).

Results

Fish samples

Fishes used to provide end-member values were identified as marine and freshwater residents, all individuals being adult (Table 1). The target species (*L. lentjan*) collected from the lagoon ranged in size from 70 to 145 mm TL, four specimens (135–145 mm TL) being subadult. Conversely, *L. lentjan* collected from CARs varied in size from 154 to 452 mm TL (Table 2), the three smallest samples (154–184 mm TL) being considered subadult. The overall pool of *L. lentjan* from the lagoon and CARs showed a significant relationship between TL and otolith length ($R^2 = 0.96$, $P < 0.001$), suggesting that increasing otolith size was consistent with fish growth.

Relationship between $\delta^{18}\text{O}_{\text{water}}$ and salinity regimes

At salinities of 33, 32.5, 21.8, 9.7 and 0 PSU, mean (\pm s.d. of triplicate measurements) $\delta^{18}\text{O}_{\text{water}}$ values were -0.42 ± 0.01 , -0.47 ± 0.02 , -2.00 ± 0.02 , -4.11 ± 0.02 and $-5.83 \pm 0.04\text{‰}$ (SMOW) respectively (Fig. 3). Seawater and freshwater salinity differed by 33 PSU, corresponding to 4.7‰ SMOW in $\delta^{18}\text{O}_{\text{water}}$. A significant positive linear relationship was found between ambient water salinity and $\delta^{18}\text{O}_{\text{water}}$ from the study areas ($R^2 = 0.9992$; $P < 0.0001$).

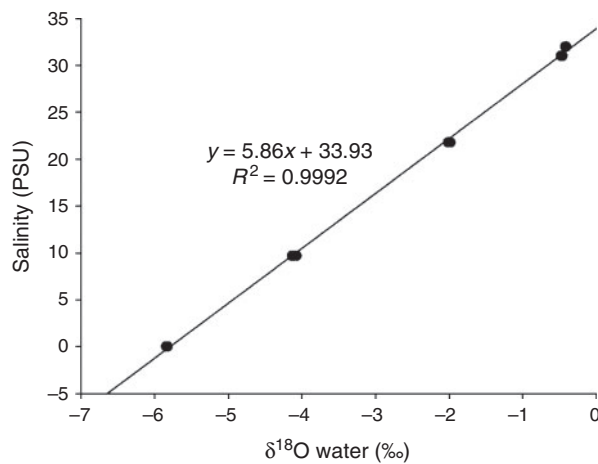
Stable isotopes in potential food items compared between the lagoon and CARs

There were different trends in stable isotope values of potential food items between the lagoon and CARs. Although the food items in the lagoon were enriched in ^{15}N and depleted in ^{13}C in both seasons, in CARs the reverse was observed, namely depletion in ^{15}N and enrichment in ^{13}C (Fig. 4). Significant differences were also found in both $\delta^{13}\text{C}_{\text{food}}$ and $\delta^{15}\text{N}_{\text{food}}$ between the lagoon and CARs (Kruskal–Wallis test, $P < 0.001$). In addition, a small but non-significant difference was found in the isotope composition of food items in the lagoon between seasons.

Table 2. Stable isotope values (‰ mean \pm s.d.) in otoliths and muscle tissue of *Lethrinus lentjan* from the Setiu Lagoon and CARs

Data are given as the mean \pm s.d. 'Post-larval' and 'margin' correspond to juvenile and adult sections of adult fish respectively. CARs, coastal artificial reefs; TL, total length; J, juvenile; Sa, subadult; A, adult

Habitat	Time	Otolith				Muscle		TL (cm)	Stage
		$\delta^{13}\text{C}$ (‰)		$\delta^{18}\text{O}$ (‰)		$\delta^{15}\text{N}$ (‰)	$\delta^{13}\text{C}$ (‰)		
		Post-larval	Margin	Post-larval	Margin				
Setiu Lagoon	January 2016		-6.9 ± 0.5		-49 ± 02	11.2 ± 0.1	-16.3 ± 0.2	11.9 ± 2.1	J and Sa
	July 2016		-7.3 ± 0.8		-31 ± 03	11.2 ± 0.3	-19.3 ± 0.5	11.1 ± 3.2	J and Sa
	July 2017		-6.6 ± 0.4		-36 ± 02	10.0 ± 0.2	-17.9 ± 0.9	11.1 ± 0.9	J
CARs	April	-4.9 ± 1.0	-4.5 ± 1.1	-2.7 ± 0.4	-26 ± 05	9.9 ± 0.6	-14.5 ± 0.9	25.2 ± 8.0	Sa and A
	August	-5.5 ± 1.4	-3.2 ± 1.3	-2.6 ± 0.4	-21 ± 02	9.5 ± 0.8	-14.7 ± 0.9	30.3 ± 8.4	Sa and A

**Fig. 3.** Linear regression between salinity (practical salinity units, PSU) and $\delta^{18}\text{O}$.

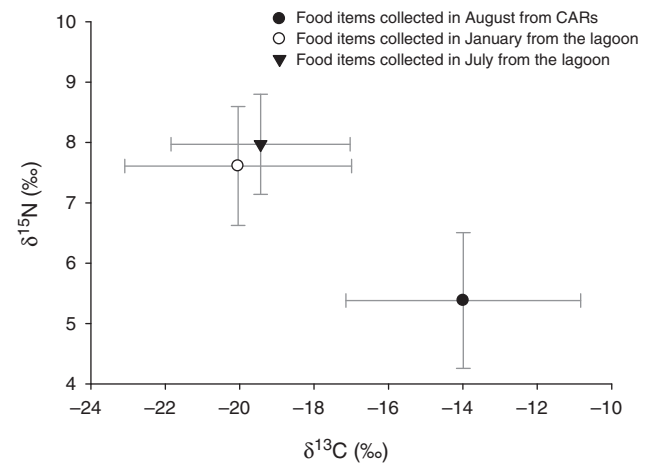
Stable isotopes in fish muscle tissue

The $\delta^{13}\text{C}_{\text{muscle}}$ values exhibited a gradient from freshwater to marine fishes, the most depleted $\delta^{13}\text{C}_{\text{muscle}}$ values being found in freshwater residents, whereas marine residents had the highest $\delta^{13}\text{C}_{\text{muscle}}$ values (t -test, $P < 0.001$). The wide range of $\delta^{15}\text{N}_{\text{muscle}}$ values among fish residents likely reflects different feeding modes and trophic levels, as well as different nitrogen sources in the ecosystem (Table 1).

In the lagoon, significant differences in $\delta^{13}\text{C}_{\text{muscle}}$ of *L. lentjan* occurred between seasons and sites (one-way ANOVA, Tukey's honest significant difference (HSD), $P < 0.05$), but a significant difference in $\delta^{15}\text{N}_{\text{muscle}}$ values was only found between sites (one-way ANOVA, Tukey's HSD, $P < 0.05$; Table 2).

Comparisons of stable isotope signatures in *L. lentjan* between inshore and offshore indicated that the $\delta^{13}\text{C}_{\text{muscle}}$ values were more depleted in fish from the lagoon than from CARs (t -tests, $P < 0.001$), whereas the $\delta^{15}\text{N}_{\text{muscle}}$ values were more enriched for lagoon-captured fish than in those from CARs (t -tests, $P < 0.001$; Table 2).

There was a significant positive relationship between $\delta^{13}\text{C}_{\text{muscle}}$ and TL for fish captured in CARs had ($R^2 = 0.40$, $P < 0.001$; Fig. 5). However, a negative relationship found

**Fig. 4.** $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (mean \pm s.d., ‰) of potential food items from coastal artificial reefs (CARs) and the lagoon.

between $\delta^{15}\text{N}_{\text{muscle}}$ and TL that was not significant ($R^2 = 0.15$, $P = 0.085$; Fig. 5).

Otolith analysis of end-member habitat patterns

The $\delta^{13}\text{C}_{\text{otolith}}$ and $\delta^{18}\text{O}_{\text{otolith}}$ values discriminated between end-member patterns (Table 1), with values for freshwater residents ranging from -19.9 to -10.7 and from -7.9 to -5.7 ‰ respectively, compared with more enriched values for marine residents, which ranging from -8.6 to -3.8 ‰ for $\delta^{13}\text{C}_{\text{otolith}}$ and from -2.3 to -1.7 ‰ for $\delta^{18}\text{O}_{\text{otolith}}$ (Fig. 6). The OSI values for the brackish water resident *A. hyalosoma* were intermediate between freshwater and marine residents, ranging from -9.3 to -5.2 ‰ for $\delta^{13}\text{C}_{\text{otolith}}$ and from -5.0 to -2.8 ‰ for $\delta^{18}\text{O}_{\text{otolith}}$ (Fig. 6). The mean ranges of $\delta^{13}\text{C}_{\text{otolith}}$ and $\delta^{18}\text{O}_{\text{otolith}}$ within marine and freshwater resident fishes were 9.7 and 4.5 ‰ respectively, the latter being close to 4.7 ‰ SMOW determined for $\delta^{18}\text{O}_{\text{water}}$.

Otolith analyses of *L. lentjan*

In the lagoon, the juvenile $\delta^{13}\text{C}_{\text{otolith}}$ and $\delta^{18}\text{O}_{\text{otolith}}$ values ranged from -8.1 to -5.9 ‰ and from -5.1 to -2.8 ‰ respectively, having a similar range to the brackish-water resident *A. hyalosoma*. Comparisons of juveniles between seasons and sites revealed that $\delta^{13}\text{C}_{\text{otolith}}$ values generally had a similar range

between seasons, but were significantly different between sites (Table 3), whereas $\delta^{18}\text{O}_{\text{otolith}}$ values were lowest in January 2016 compared with both July 2016 and July 2017 (Table 3). In the CARs, OSI values for juvenile portions ranged from -7.9 to -3.0‰ ($\delta^{13}\text{C}_{\text{otolith}}$) and from -3.4 to -1.9‰ ($\delta^{18}\text{O}_{\text{otolith}}$), whereas $\delta^{13}\text{C}_{\text{otolith}}$ and $\delta^{18}\text{O}_{\text{otolith}}$ for adult portions ranged from -5.3 to -1.7‰ and from -3.5 to -1.7‰ respectively. There were no significant differences in either isotope

value of juvenile portions between August and April, although significant differences in $\delta^{13}\text{C}_{\text{otolith}}$ and $\delta^{18}\text{O}_{\text{otolith}}$ of adult portions were found between sampling periods (t -test, $P = 0.018$ for $\delta^{13}\text{C}_{\text{otolith}}$; U -test, $P = 0.009$ for $\delta^{18}\text{O}_{\text{otolith}}$). The juvenile portions showed significantly more depletion of $\delta^{13}\text{C}_{\text{otolith}}$ and $\delta^{18}\text{O}_{\text{otolith}}$ than adult portions in August (t -test, $P = 0.001$ for both). There was a slight depletion of stable isotope signature in juvenile portions compared with adult portions in April, but the difference

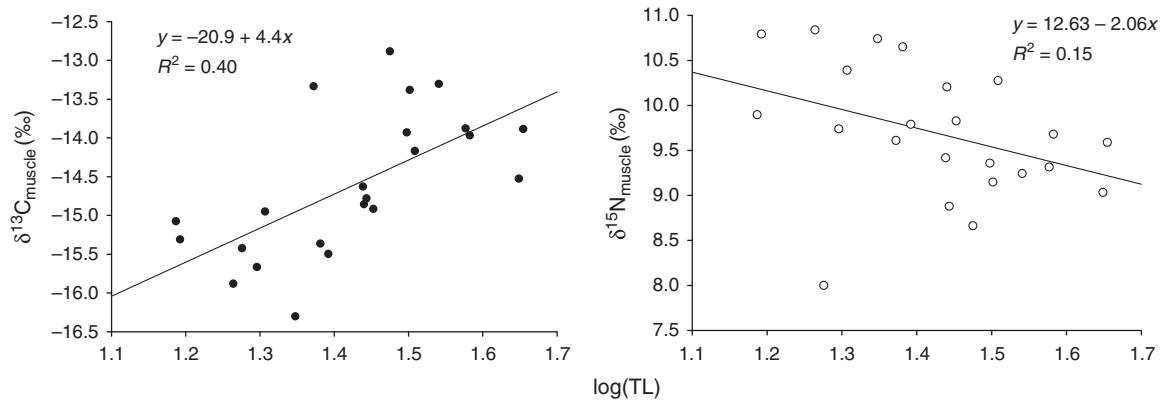


Fig. 5. Linear regression between $\delta^{13}\text{C}_{\text{muscle}}$ and $\delta^{15}\text{N}_{\text{muscle}}$ values of adult *Lethrinus lentjan* from coastal artificial reefs and total length (cm).

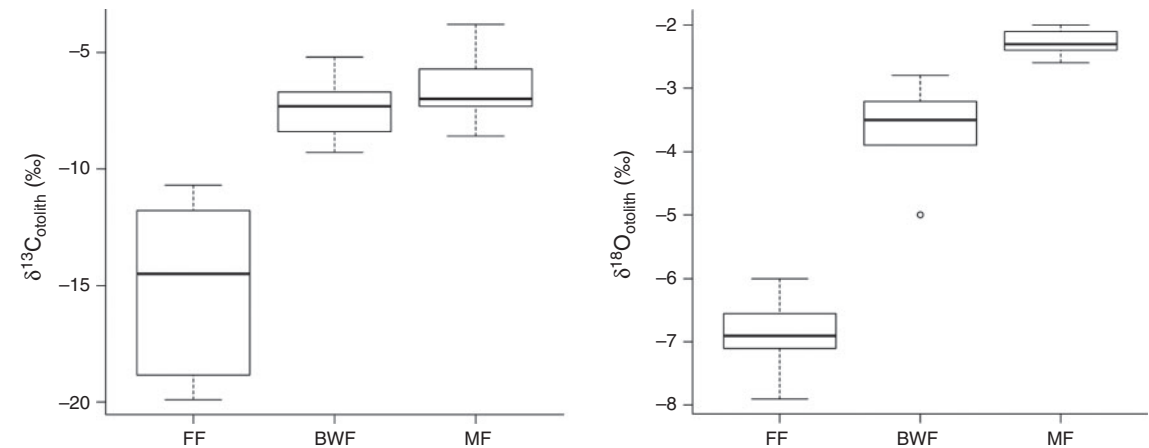


Fig. 6. Variations in $\delta^{13}\text{C}_{\text{otolith}}$ and $\delta^{18}\text{O}_{\text{otolith}}$ in adult fish occupying different habitats. The boxes show the interquartile range, with the median value indicated by the horizontal line; whiskers show the range. MF, marine fish (end-member); FF, freshwater fish (end-member); BWF, brackish-water fish.

Table 3. Results of one-way analysis of variance performed on stable isotope signatures among fish otolith samples
MS, mean square

		d.f.	MS	F	P-value	Sources	P-value (Tukey's test)
$\delta^{13}\text{C}$	Between groups	2	1.338	6.75	0.011	Site 1_July v. Site 2_July	0.011
	Within groups	12	0.198			Site 1_July v. Site 1_January	0.088
	Total	14				Site 2_July v. Site 1_January	0.433
$\delta^{18}\text{O}$	Between groups	2	4.345	66.16	<0.0001	Site 1_July v. Site 2_July	0.012
	Within groups	12	0.066			Site 1_July v. Site 1_January	<0.0001
	Total	14				Site 2_July v. Site 1_January	<0.0001

did not reach statistical significant (t -test, $P = 0.416$ for $\delta^{13}\text{C}_{\text{otolith}}$; $P = 0.654$ for $\delta^{18}\text{O}_{\text{otolith}}$). The three small adult fish (<185 mm TL) similarly exhibited the lowest range of $\delta^{18}\text{O}_{\text{otolith}}$ values in both portions (varying between -3.7 and -2.8‰ for adult portions, and between -3.4 and -2.8‰ for juvenile portions) in the same individuals, but the $\delta^{13}\text{C}_{\text{otolith}}$ for these fish did not show any overlap with juveniles from Setiu Lagoon. These results suggest that small adult fish may freshly recruit to CARs after their ontogenetic migration from brackish-water habitats. Seven of the samples had $\delta^{18}\text{O}_{\text{otolith}}$ values ranging between -2.4 and -1.8‰ in both portions (Fig. 7). Interestingly, a higher number of juvenile portions exhibited $\delta^{18}\text{O}_{\text{otolith}}$ values close to those of juveniles collected in July (both 2016 and 2017; corresponding to SWM), whereas no juvenile portion $\delta^{18}\text{O}_{\text{otolith}}$ value fell within the $\delta^{18}\text{O}_{\text{otolith}}$ range of juveniles collected in January 2016 (corresponding to NEM; Fig. 7).

MANOVA indicated significant differences in OSI signatures between juveniles from the lagoon and juvenile portions from CARs (Wilks' $\lambda = 0.083$; $F = 19.21$; $P < 0.0001$). The results of univariate and multiple comparisons confirmed that differences among sampling periods were significant for both elements (Table 4; see Table S1, available as Supplementary material to this paper).

Discussion

In this study both muscle and otolith stable isotopes were used to identify short- and long-term fish movements across

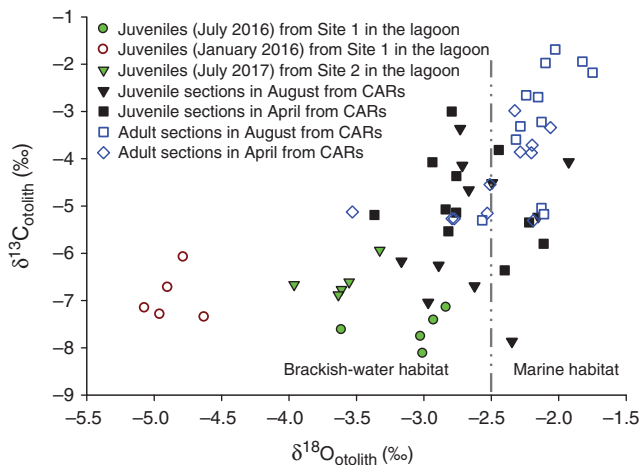


Fig. 7. Scatterplot of $\delta^{13}\text{C}_{\text{otolith}}$ and $\delta^{18}\text{O}_{\text{otolith}}$ values in different fish groups. The vertical dashed line indicates separation of $\delta^{18}\text{O}$ areas (2.5‰) into brackish-water and marine habitats. CARs, coastal artificial reefs.

habitats. For muscle stable isotope, because of fish muscle-tissue turnover rate, movement patterns covered a few weeks to months (Herzka 2005; Xia *et al.* 2013), the gradual change in stable isotopes in tissues being related to size-dependent (growth) fish movement recorded across habitats or diet shifts (Vaslet *et al.* 2011; Le *et al.* 2018) or seaward migration (Cocheret de la Morinière *et al.* 2003; Nakamura *et al.* 2008; Berkström *et al.* 2012, 2013; Huijbers *et al.* 2015). Given the size at first maturity (L_{50}) of *L. lentjan* in seagrass beds, individuals could ontogenetically move to coral reef adult habitats at a size of ~ 140 mm TL (Kimirei *et al.* 2013a). Earlier studies have found that there were no adult fish in the lagoon and that juvenile fish ontogenetically shifted diet and habitat in a size range >120 mm TL (Le *et al.* 2018). Potential food sources also showed differences in stable isotopes between the lagoon and CAR habitats, similar isotopic gradients among habitats having been reported from other tropical coasts (Cocheret de la Morinière *et al.* 2003; Nakamura *et al.* 2008). Hence, the depleted ^{13}C and enriched ^{15}N signatures of small adult individuals (<185 mm TL) in CARs suggest that they are recent arrivals from estuarine habitats.

One of the biggest challenges to retrospectively identify fish lifetime movements among habitats is the unknown environment to which the fish has been exposed during different life stages. The $\delta^{13}\text{C}_{\text{otolith}}$ and $\delta^{18}\text{O}_{\text{otolith}}$ fingerprints can be used as proxies of temperature or salinity to reconstruct the past environments of migratory fish, because variations in these isotopic signatures have been shown experimentally to be significantly related to temperature or salinities (Elsdon and Gillanders 2002; Kerr *et al.* 2007; McMahon *et al.* 2011; Shirai *et al.* 2018). Because $\delta^{13}\text{C}_{\text{otolith}}$ values can be affected by several factors, including DIC incorporated into otoliths derived from ambient waters (Weidman and Millner 2000; Solomon *et al.* 2006; Tohse and Mugiya 2008; Elsdon *et al.* 2010), species-specific differences in carbon metabolism (Weidman and Millner 2000) and dietary sources (Schwarcz *et al.* 1998; McMahon *et al.* 2011), changes in $\delta^{13}\text{C}_{\text{otolith}}$ provide some ability to differentiate between large trophic- and ecosystem-level shifts, related to inshore–offshore carbon sources or depth gradients of DIC in $\delta^{13}\text{C}_{\text{otolith}}$ values (Mulcahy *et al.* 1979; Schwarcz *et al.* 1998). In the present study, the increasing trend of $\delta^{13}\text{C}_{\text{otolith}}$ values from small (young) fish to large (old) fish was partly consistent with the hypothesis of movement of fish to deeper offshore waters where the $\delta^{13}\text{C}$ of DIC is lower compared with inshore wetlands and changes in nutrient sources in new habitats (Bouillon *et al.* 2011). However, a part of this trend in $\delta^{13}\text{C}_{\text{otolith}}$ values could also be explained by a reduction in mass-specific field

Table 4. Univariate test results of multivariate analysis of variance performed on stable isotope signatures among fish otolith samples
OSI, otolith stable isotope; SS, sum of squares; MS, mean square

Source	OSI	SS	d.f.	MS	<i>F</i>	<i>P</i> -value
Contrast	$\delta^{13}\text{C}$	35.635	4	8.909	8.782	<0.0001
	$\delta^{18}\text{O}$	21.822	4	5.456	49.331	<0.0001
Error	$\delta^{13}\text{C}$	32.462	32	1.014		
	$\delta^{18}\text{O}$	3.539	32	0.111		

metabolic rates with fish growth during the lifetime (Schwarcz *et al.* 1998; Jamieson *et al.* 2004; Trueman *et al.* 2016). Several studies have successfully used $\delta^{18}\text{O}_{\text{otolith}}$ as a proxy of salinity or temperature to retrospectively identify habitat use in coastal fishes (Elsdon and Gillanders 2002; Kerr *et al.* 2007; McMahon *et al.* 2011; Shirai *et al.* 2018), because lower $\delta^{18}\text{O}_{\text{otolith}}$ values indicate high temperatures and low salinity, and vice versa (Campana 1999; Weidman and Millner 2000; Kitagawa *et al.* 2013; Shirai *et al.* 2018). However, in the tropical zone, particularly the ECPM, seawater temperatures often vary narrowly (1–3°C) on the surface and in the water column throughout the seasons (Akhir 2012; Akhir *et al.* 2014; Daryabor *et al.* 2015). Given that water temperatures in rivers could also be affected by rainfall in the NEM season and upstream water input, annual mean temperature nevertheless varied within 3°C in the study area (Suratman *et al.* 2015). Furthermore, a change in temperature by 1°C causes isotopic fractionation of $\sim 0.22\text{--}0.25\text{‰}$ during aragonite precipitation (Kim *et al.* 2007b). It is reasonable to estimate that the effect of temperature change on $\delta^{18}\text{O}_{\text{otolith}}$ is less than 1.0‰ (corresponding to $\sim 3^\circ\text{C}$ in water), whereas in the present study end-member species showed enriched $\delta^{18}\text{O}_{\text{otolith}}$ from freshwater to seawater (the difference in $\delta^{18}\text{O}_{\text{otolith}}$ was $\sim 4.5\text{‰}$, close to 4.7‰ SMOW in $\delta^{18}\text{O}_{\text{water}}$). It is likely that variations in $\delta^{18}\text{O}_{\text{otolith}}$ between and within species in the present study were affected more by salinity than by temperature. Because the enriched $\delta^{18}\text{O}$ signatures of pelagic oceanic water vary slightly within $\pm 0.5\text{‰}$ worldwide, most freshwater bodies can be highly isotopically depleted (Craig 1961; Dansgaard 1964; Schaffner and Swart 1991; Rohling 2013; Shirai *et al.* 2018). Accordingly, the mixing of run-off water (riverine waters and precipitation) with ocean water (mixed masses of water) in coastal regions may be expected to form a positive gradient in $\delta^{18}\text{O}_{\text{otolith}}$ values from fishes in fresh water to fishes in marine water habitats. In addition, $\delta^{18}\text{O}_{\text{otolith}}$ has exhibited quasi-linear relationships with salinity under both experimental conditions (Kalish 1991; Thorrold *et al.* 1997) and in the field (Weidman and Millner 2000). In addition, $\delta^{18}\text{O}_{\text{otolith}}$ values may be affected by species-specific fractionation, such variations estimated as $\sim 1\text{‰}$ by Sakamoto *et al.* (2017) and Shirai *et al.* (2018). Hence, salinity is reasonable as the dominant parameter for reconstructing the past environment of *L. lentjan*.

For adult *L. lentjan*, no significant difference in OSI values in juvenile portions between sampling periods suggests that these fishes may have been exposed to similar environments as juveniles, whereas the difference in both OSI values in adult portions between sampling periods indicates that the fish may have been exposed to changes in ambient environment or food resources related to current circulation patterns driven by monsoonal seasons. Indeed, water masses off the Terengganu coast have had small changes reported in both salinity and temperature (nearly 1.0 PSU and 1.5°C) between monsoonal seasons (Akhir *et al.* 2014). Such changes in the ambient environment could be recorded in the otolith chemistry, even if the adult fish remains in the CARs, because the $\delta^{13}\text{C}_{\text{otolith}}$ would be primarily affected by DIC in different waters or food availability, whereas $\delta^{18}\text{O}_{\text{otolith}}$ reflects exposure to water temperatures and salinities of different provenance (Ashford and

Jones 2007). Furthermore, the ‘spillover’ effect can be considered as another factor replenishing adult populations in the CARs, because some adults may come from adjacent natural coral reefs of MPAs to form mating groups or seeking food sources (Carr *et al.* 2017), the former being related to the spawning season (April–June; Grandcourt *et al.* 2011).

Conversely, several juvenile portions showed lower $\delta^{18}\text{O}_{\text{otolith}}$ values than adult portions from the same individuals in August, suggesting that these fish may have inhabited estuarine waters during their juvenile phase. Furthermore, the otolith of small adult fish had narrow adult zones beyond the post-larval period, the drilled samples taken from otolith edges potentially including a mix of new (seawater) and old (brackish water) material deposited during otolith formation soon after the fish arrived at the CAR. The former included primarily isotope signatures of marine waters (enriched OSI values) in the upper layers, whereas the latter corresponded to estuarine waters (depleted OSI values) in the lower layers. Hence, the small adult fish ($< 185\text{ mm TL}$) had the lowest $\delta^{18}\text{O}_{\text{otolith}}$ signatures with characteristics of fish inhabiting estuarine waters (depleted $\delta^{18}\text{O}_{\text{otolith}}$), which supports population connectivity between estuarine and marine habitats. Alternatively, juvenile and adult portions in the same fish exhibited $\delta^{18}\text{O}_{\text{otolith}}$ values similar to marine residents (noted in seven individuals), suggesting that some individual *L. lentjan* may not spend their juvenile phases in shallow estuarine habitats, instead possibly being self-replenishing in the reef habitats or migrating from surrounding coral reefs. This result is consistent with a previous study that showed that some *L. lentjan* adults had never passed through brackish-water vegetation habitats as juveniles, instead inhabiting predominantly coral reefs during their entire life (Kimirei *et al.* 2013b).

For juvenile emperors from the lagoon, the overall more negative $\delta^{18}\text{O}_{\text{otolith}}$ values in juvenile fish collected in January may reflect the influence of changing water composition during the NEM season, due to the input of fresh water from precipitation and tributaries potentially affecting isotope signatures of water in the lagoon (Cocheret de la Morinière *et al.* 2003). Furthermore, the effects of unfavourable environmental conditions during peak rainfall in the NEM may force the juvenile reef fish to emigrate or to go deeper in the lagoon because they may have certain salinity tolerances and preferences (Estudillo *et al.* 2000; Serrano *et al.* 2010). Unlike $\delta^{18}\text{O}_{\text{otolith}}$, a small variation in $\delta^{13}\text{C}_{\text{otolith}}$ between seasons may not only reflect a change in water composition, because $\delta^{13}\text{C}_{\text{otolith}}$ values can be affected by several factors (see above), but may also be related to differences in metabolic rates due to seasonal temperature changes (Kalish 1991; Trueman *et al.* 2016). Therefore, interannual variability in OSI ($\delta^{13}\text{C}$ and $\delta^{18}\text{O}$) values may provide baseline information on the typical nursery habitat of fish. Such information may be valuable for extrapolation to retrospectively track nursery habitats of adult *L. lentjan* when OSI signatures are compared between juvenile portions of adult fishes from CARs and juvenile fishes from the lagoon. As indicated by the MANOVA, there were offsets in OSI signatures between juvenile portions of adult fish and juvenile fish, suggesting that Setiu Lagoon may not be an important juvenile area for the fish sampled from CARs (Fig. 7). This result may account for the influence of coastal currents when the fish ontogenetically migrate out of the lagoon. The different velocity of coastal

currents between monsoonal seasons could profoundly affect the direction of fish migration from inshore to offshore habitats (Carr *et al.* 2017). Indeed, strong currents that flow southward along the coast during the NEM could have deflected the movement of juveniles to CARs, promoting southward connectivity instead. Accordingly, only a limited number of juvenile fish could successfully recruit to the CARs from the lagoon. This explanation may also be consistent with isotope values in juvenile portions of some adult individuals being outside the isotope range in juveniles collected from the lagoon, whereas a separation in $\delta^{13}\text{C}_{\text{otolith}}$ among individuals could be attributed to spatial differences in habitat use (Mateo *et al.* 2010; Pruett *et al.* 2010; Kimirei *et al.* 2013b). Thus, the adult fish are considered a mix of cohorts replenished by different nursery habitats. Conversely, low-intensity coastal currents and weak northward currents that flow along the coast during the short inter-monsoon periods and SWM respectively may not significantly obstruct direct offshore migration of juvenile fish to CARs from the lagoon. Although very limited information is available on the effects of ocean circulation on fish migration in the South China Sea, a few studies have reported on the effects of ocean currents on landfall latitudes and migration speed of migratory fish, such as salmon returning to parental spawning grounds (Thomson *et al.* 1992).

In conclusion, although we could not find clear isotopic evidence of population connectivity between the Setiu Lagoon and CARs by ontogenetic migration of *L. lentjan*, artificial reef deployments may benefit adult fish populations after ontogenetic migration from other nursery habitats along the coast. Thus, given that Setiu Lagoon may be insufficient as a single nursery habitat for maintaining fish stocks, it is recommended that multiple nursery habitats along the coastal region of the study be included in any conservation strategy. Future multidisciplinary studies should be performed to investigate potential nursery habitats along the coast and to clarify the effects of coastal currents on the contribution of juvenile biomass to adult populations in the CARs and natural coral reefs along ECPM. Such information would be critical for the effective design of a sustainable resources management program for the coastal region, particularly concerning the linkage between inshore nurseries and oceanic habitats.

Conflicts of interest

The authors declare that they have no conflicts of interest.

Declaration of funding

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