

Facultative habitat selection in Pacific tarpon *Megalops cyprinoides* as revealed by otolith Sr:Ca ratios

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ABSTRACT: The Pacific tarpon *Megalops cyprinoides* is a euryhaline fish that is widely distributed in offshore waters of the tropical and subtropical Indo-Pacific Ocean. It spawns in offshore waters and the larvae drift with tidal currents before recruiting to estuarine nursery areas at ~25 to 30 d post-hatching. Young Pacific tarpon are found in coastal waters, rivers, estuaries, inner bays, and mangrove areas. However, their age-specific migratory behavior and habitat selection are still unclear. The strontium (Sr) concentration in seawater is ~100× higher than in fresh water, and the Sr:Ca ratios in fish otoliths are positively correlated with ambient salinity and are thus widely used in studying fish migration between seawater and freshwater environments. To understand the migratory environmental history of the Pacific tarpon, otolith Sr:Ca ratios of leptocephali collected from the estuary and sub-adults collected from both Tadu Creek and offshore waters on the west coast of Taiwan were examined using an electron probe microanalyzer (EPMA). Fish were aged by counting otolith annuli. The Sr:Ca ratios in leptocephalus otoliths were high ($7.4 \pm 0.03 \times 10^{-3}$). However, the patterns of otolith Sr:Ca ratios in 1 to 3 yr old sub-adults were diverse and can be divided into 3 types: largely brackishwater residents, largely freshwater residents, and vagrants between brackish and fresh waters. Fish older than 4 to 5 yr all return to the marine environment. This study demonstrates that habitat selection in the Pacific tarpon after the leptocephalus stage is facultative and that their migratory environmental history can be reconstructed from otolith Sr:Ca ratios.

KEY WORDS: *Megalops cyprinoides* · Pacific tarpon · Leptocephalus · Otolith · Sr:Ca ratio

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INTRODUCTION

The family Megalopidae has 2 species of tarpon: the Pacific tarpon *Megalops cyprinoides* (Broussonet 1782) of the Indo-Pacific Ocean and the Atlantic tarpon *Megalops atlanticus* (Valenciennes 1847) of the Atlantic Ocean. Both species have a leptocephalus stage in their early life, as do other members of the Superorder Elopomorpha (Elopiformes, Albuliformes, Anguilliformes and Saccopharyngiformes) (Hulet & Robin 1989). The tarpon is the most primitive of the Elopomorpha (Tsukamoto & Okiyama 1997, Wang et al. 2003) and also the most ancestral among teleost fishes, as evi-

denced by its morphological features and results of molecular study (Forey et al. 1996). Tarpon have a modified air bladder that allows them to inhale atmospheric oxygen and tolerate oxygen-poor environments (Wells et al. 2003). This enables them to live in polluted environments, and makes them useful as an indicator species for heavy stream pollution (Wang 2002). Although both species of tarpon are marine spawners, they can tolerate a wide range of salinities. After hatching, tarpon larvae are advected to an inshore nursery area ~25 to 30 d later (Tzeng et al. 1998) and after metamorphosing, young tarpon are frequently found in rivers, bays, mangrove areas and even in the upper reaches

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of rivers (Merrick & Schmida 1984, Tzeng & Yu 1986, Coates 1987).

During spring and until late summer, large numbers of metamorphosing Pacific tarpon leptocephali are found schooling in the estuaries of western Taiwan (Tzeng et al. 2002b). However, little is known about their migratory history and habitat selection (Tsukamoto & Okiyama 1993, 1997). As such, it is unknown whether Pacific tarpon obligate or facultative migratory fishes after the leptocephalus stage.

Fish migratory behavior and habitat selection usually change with life stage (Secor 1992). Such information can be retrieved using different means that include traditional census of tagged individuals (Zeller & Russ 2000), advanced tagging and marking techniques, acoustic, archival and satellite tagging (Sedberry & Loefer 2001) and use of natural markers such as chemical signatures within calcified structures like fish otoliths (Secor & Rooker 2000, Tsukamoto & Arai 2001, Tzeng et al. 2007).

Fish otoliths are primarily composed of calcium carbonate with minor organic matrices that are deposited on a daily basis (Pannella 1971, Campana & Neilson 1985, Jones 1986), which permit the determination of daily fish age. The use of calcium (Ca) together with elements deposited in otolith increments enables the reconstruction of the past migratory environmental history of fish (Secor 1992, Bath et al. 2000). At least 31 elements have been found in fish otoliths (Campana 1999) and among these elements, strontium (Sr) and calcium are widely used in determining migratory history. Strontium ions have the same valence and similar ionic radius as calcium ions and are readily incorporated into aragonite otolith by substitution for calcium (Amiel et al. 1973). The Sr concentration in seawater is 100× higher than in fresh water (Campana 1999, Milton & Chenery 2001), permitting the use of otolith Sr:Ca ratios as a natural marker for examining the migratory environmental history, life history strategies and migratory behavior of diadromous fishes (Kalish 1990, Secor et al. 1995, Tzeng et al. 1997, Tsukamoto & Arai 2001). The relationship between the Sr:Ca ratio in tarpon otolith and the ambient salinity after metamorphosis was validated by Chen et al. (2008) using wild-caught leptocephali reared in different salinities. Therefore, the migratory behavior and habitat selection of the Pacific tarpon can be reconstructed from otolith Sr:Ca profiles.

The aims of the present study were to use otolith microchemistry to clarify the migratory behavior of the Pacific tarpon between freshwater and marine habitats by analyzing temporal changes in Sr:Ca ratio in the otolith using an electron probe microanalyzer (EPMA). Fish age was determined by counting otolith annuli to evaluate whether habitat selection is age-specific.

MATERIALS AND METHODS

Sampling design. A total of 1106 tarpon leptocephali were collected from the estuary of Tadu Creek in 1998, 62 sub-adults were collected from the freshwater area of the lower (LT, $n = 54$) and middle (MT, $n = 8$) reaches of Tadu Creek from 1998 to 1999, and 19 sub-adults were collected in the offshore waters adjacent to Tadu Creek in 2004 to 2005 (Fig. 1). The leptocephali were collected using a net set against the tidal current in the estuary, while the sub-adults from the lower and middle reaches of Tadu Creek were collected using a trammel net (50 m long × 1.5 m wide) with 3 layers of different mesh sizes (15–20–15 cm). Sub-adults were collected during the daytime monthly from March 1998 through March 1999. Two to 4 hauls from the middle and lower reaches of Tadu Creek were made each month. The sub-adults from offshore waters were collected using a gill net.

After collection, all specimens were preserved in ice in the field. The fork length of leptocephali and sub-adults and the body weight of sub-adults were measured to the nearest 0.1 mm and 0.01 g. The number of fish collected and biological measurements can be seen in Table 1. The gonads of sub-adult fish were visually examined to determine sex and maturation stage.

Otolith preparation for age determination. Sagittae, the biggest of the 3 pairs of otoliths, were removed from the sacculus of the inner ear. The right sagittal otolith was cleaned with distilled water, air dried, embedded in Epofix resin, ground and then polished along the sagittal plane with 0.05 μm alumina powder until the primordium was exposed. The annuli were

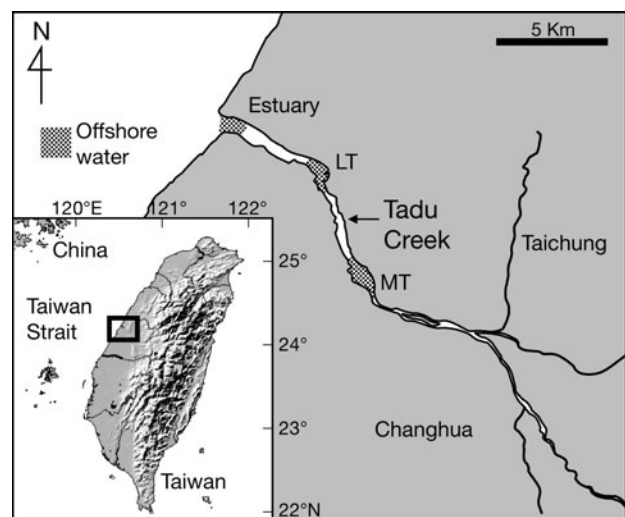


Fig. 1. Sampling locations (dotted areas) for Pacific tarpon *Megalops cyprinoides* in the estuary, the lower (LT) and middle (MT) reaches, and the offshore waters adjacent to Tadu Creek in central Taiwan

examined under a microscope with a black background to determine age. Annual rings, which are discernible as shown in Fig. 2a, were validated by counting the number of otolith daily increments between the metamorphosis check and the first annulus during the period from recruitment to the first winter (Fig. 2b). The annulus in each otolith was counted by 2 different readers. Previous studies have shown that the otolith growth increment in Pacific tarpon is deposited daily (Tsukamoto & Okiyama 1993, Chen & Tzeng 2006); thus, the daily growth increments in leptocephali otoliths were counted to determine the marine larval duration before estuarine arrival. In total, random sub-samples of 88 leptocephali and 81 sub-adults collected from fresh water ($n = 62$) and offshore waters ($n = 19$) were aged.

Measurement of otolith Sr:Ca ratios. The temporal pattern of Sr:Ca ratios (wt %) along the otolith transect was used to evaluate the environmental history of each Pacific tarpon, and the measurement procedures were similar to those used by Tzeng et al. (2002a, 2003). For comparison, 5 leptocephali were randomly selected for Sr:Ca ratio analysis, while the 81 sub-adults collected from freshwater ($n = 62$) and offshore ($n = 19$) habitats were all used in age determination and otolith Sr:Ca

ratio analyses. The otolith Sr:Ca ratios of the sub-adults were measured along the shorter posterior axis of the otolith (Fig. 2b). Otolith Sr and Ca concentrations were measured using an EPMA (JXA-8900R, JEOL) at an interval of 10 μm from the primordium to the otolith edge, with an electron beam size of $5 \times 4 \mu\text{m}^2$ rectangle, and accelerating voltage and probe current set at 15 kV and 5 nA, respectively. Strontianite ($[\text{Sr}_{0.95}\text{Ca}_{0.05}]\text{CO}_3$) and aragonite (CaCO_3) were used as standards for the calibration of Sr and Ca concentration in the otolith.

Life history determination and data analysis. An average Sr:Ca ratio of $\leq 4 \times 10^{-3}$ was considered as the criterion to discriminate freshwater from brackishwater environments of the tarpon, as validated by a salinity control experiment with tarpon reared at a salinity of 0 by Chen et al. (2008). This criterion was also supported by the average Sr:Ca ratio of $3.8 \pm 0.54 \times 10^{-3}$ calculated from the Sr:Ca ratios in the otolith edge of 62 wild sub-adult Pacific tarpon caught in the freshwater reaches of Tadu Creek. The average Sr:Ca ratio range of tarpon reared in salinities of 10 and 35 were 6×10^{-3} to 8×10^{-3} and 7×10^{-3} to 11×10^{-3} , respectively (Chen et al. 2008). Average Sr:Ca ratios $> 8 \times 10^{-3}$ were considered as the criterion separating exclusively marine and brackishwater environments. The average Sr:Ca ratio ($8.6 \pm 0.98 \times 10^{-3}$) in the otolith edge of 19 offshore sub-adults supports this criterion. Thus, tarpon with otolith Sr:Ca ratios $\leq 4 \times 10^{-3}$ were considered as freshwater residents, those with Sr:Ca ratios $> 4 \times 10^{-3}$ and $\leq 8 \times 10^{-3}$ were regarded as brackishwater residents, and those with Sr:Ca ratios $> 8 \times 10^{-3}$ were considered as seawater residents. Differences in age distribution between habitats were tested for significance using the Kolmogorov-Smirnov 2-sample test.

RESULTS

Length, weight and age of tarpon in different habitats

The fork lengths of 88 randomly selected Pacific tarpon leptocephali from the Tadu Creek estuary ranged from 21.9 to 30.2 mm. The fork length and body weight of 62 sub-adult tarpon collected in both the lower (LT) and middle (MT) reaches of Tadu Creek ranged from 174.4 to 343.7 mm and 69.38 to 558.77 g, while those for the 19 tarpon collected in waters offshore of Tadu Creek ranged

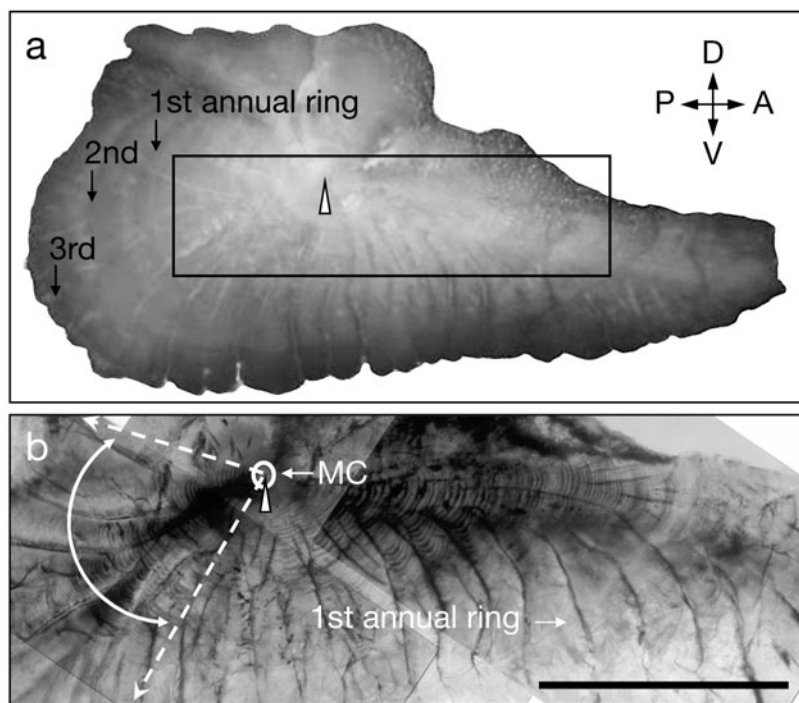


Fig. 2. *Megalops cyprinoides*. External features of the otolith and (a) annual rings under reflected light, and (b) daily growth increments and annual rings under transmitted light after polishing of a sub-adult (390 mm fork length). (Δ) Otolith primordium, MC: metamorphosis check. The area within the dashed lines indicates the location of Sr:Ca ratio analysis. A: anterior, P: posterior, D: dorsal, V: ventral. Scale bar = 1 mm

Table 1. *Megalops cyprinoides*. Range and mean (\pm SD) fork length, body weight and age by sampling site and life stage of Pacific tarpon from the Tadu Creek system and adjacent offshore waters, Taiwan. n: sample size; N/A: not available

Site	Life stage	n	Fork length (mm)		Body weight (g)		Age	
			Range	Mean \pm SD	Range	Mean \pm SD	Range	Mean \pm SD
Estuary	Leptocephalus	88	21.9–30.2	25.4 \pm 1.7	N/A	N/A	18–34 d	25.2 \pm 4.7 d
Lower and middle reaches	Young to sub-adult	62	174.4–343.7	251.7 \pm 28.4	69.38–558.77	227.88 \pm 79.34	1–3 yr	2.2 \pm 0.6 yr
Adjacent offshore	Sub-adult	19	276.6–435.1	368.2 \pm 41.1	286.82–1145.20	780.02 \pm 243.99	2–5 yr	4.1 \pm 0.9 yr

from 276.6 to 435.1 mm and 286.82 to 1145.20 g, respectively. The newly recruited leptocephali (n = 88) ranged from 18 to 34 d old, while sub-adults collected from Tadu Creek and from offshore waters were estimated to be 1 to 3 and 2 to 5 yr old, respectively (Table 1).

Temporal changes in otolith Sr:Ca ratios of leptocephali and sub-adults (ages 1 to 3) in fresh water

Sr:Ca ratios from the primordium to the otolith edge of 5 newly recruited leptocephali ranged from 5.1×10^{-3} to 10.9×10^{-3} , with a mean of $7.4 \pm 0.03 \times 10^{-3}$ (Fig. 3), indicating that they lived in a marine and brackishwater environment before estuarine arrival. Sr:Ca ratios from the primordium to the otolith edge of 5 sub-adults collected from the freshwater lower reach of Tadu Creek (LT) also ranged from 5×10^{-3} to 11×10^{-3} in the leptocephalus stage (Fig. 4). After metamorphosis, however, the patterns of Sr:Ca ratios varied greatly and can be classified into 3 types of migration behavior: Type I: largely brackishwater residents with Sr:Ca ratios that fluctuated mostly between 4×10^{-3} and 8×10^{-3} , indicating stay in a brackishwater envi-

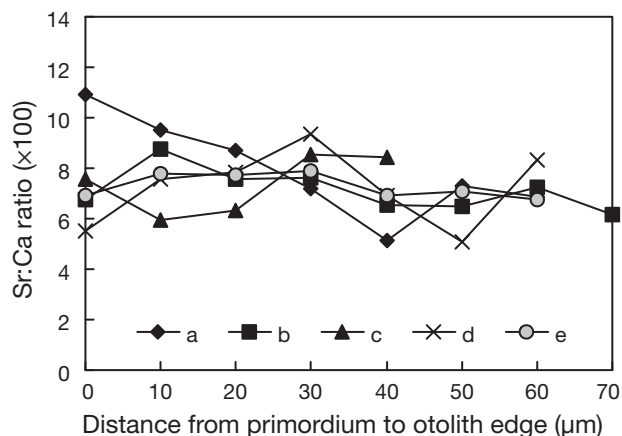


Fig. 3. *Megalops cyprinoides*. Temporal changes in otolith Sr:Ca ratios of 5 newly recruited leptocephali collected from Tadu Creek estuary. a–e: sizes in mm fork length (a: 25.8, b: 26.5, c: 25.2, d: 26.0, and e: 24.5)

ronment after metamorphosis but with possible occasional invasion of marine or fresh waters (exhibited by 12 out of 54 ind.; Fig. 4a,b); Type II: largely freshwater residents, with Sr:Ca ratios mostly $< 4 \times 10^{-3}$, indicating stay in fresh water after metamorphosis but with possible occasional invasion of brackish waters (exhibited by 34 out of 54 ind.; Fig. 4c,d); and Type III: vagrants that migrated between fresh and brackish waters for longer periods after metamorphosis (exhibited by 8 out of 54 ind.; Fig. 4e). Tarpon collected in the middle reach of Tadu Creek (MT), however, did not have Type I residents. Out of 8 ind., 6 were Type II (e.g. Fig. 5a,b) and 2 were Type III vagrants (Fig. 5c,d).

Temporal changes in otolith Sr:Ca ratios of sub-adults (ages 2 to 5) in offshore waters

Otolith Sr:Ca ratios from the primordium to the edge for 18 of the 19 tarpon collected in waters offshore of Tadu Creek ranged from 4.8×10^{-3} to 12.8×10^{-3} in the leptocephalus stage, except for some individuals where the marine larval stage was not measured. The tarpon caught in offshore waters were all Type III because after 2 to 3 yr, most fish gradually moved to the marine environment regardless of their earlier migratory type. For example, tarpon of Type I for the first 2 yr might gradually go back to the sea (Fig. 6a–c) or move to fresh water for a period before finally going back to the sea (Fig. 6d,e). Fig. 6f–o are examples of Type II tarpon for the first 1 to 3 yr that stayed in brackish water for another 1 to 2 yr and then went back to seawater (Fig. 6f–n), except for 1 ind. that went back to the sea for a period and then back to fresh water before finally going to brackish and seawater (Fig. 6o). Fig. 6p–r are examples of Type III tarpon for the first year. One individual frequently migrated between fresh and brackish water during its first year, and did not move to seawater until its 4th year (Fig. 6p). Another 2 ind. were also vagrants between fresh and brackish waters during their first year that stayed in the freshwater environment for another 1 to 3 yr before finally moving back to seawater quickly (Fig. 6q,r).

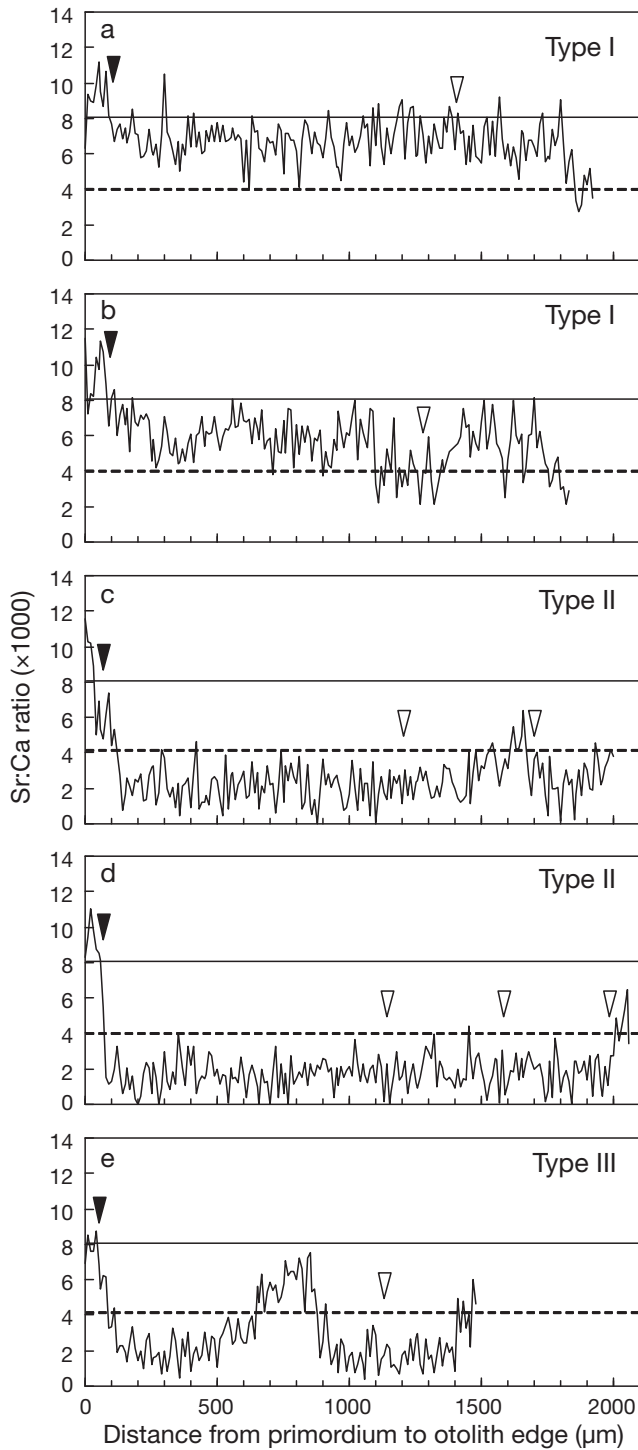


Fig. 4. *Megalops cyprinoides*. Temporal changes in otolith Sr:Ca ratios of young Pacific tarpon collected in the freshwater lower reach of Tadu Creek (LT in Fig. 1). (a) 208.3, (b) 190, (c) 225.5, (d) 287.9, and (e) 174.9 mm fork length. (▼) Metamorphosis check; (▽) annual rings. The freshwater–brackishwater boundary (dashed lines) was set at 4×10^{-3} , while the brackish–seawater boundary (solid lines) was 8×10^{-3} . Type I: brackish-water residents; Type II: freshwater residents; Type III: vagrants between brackish and fresh waters

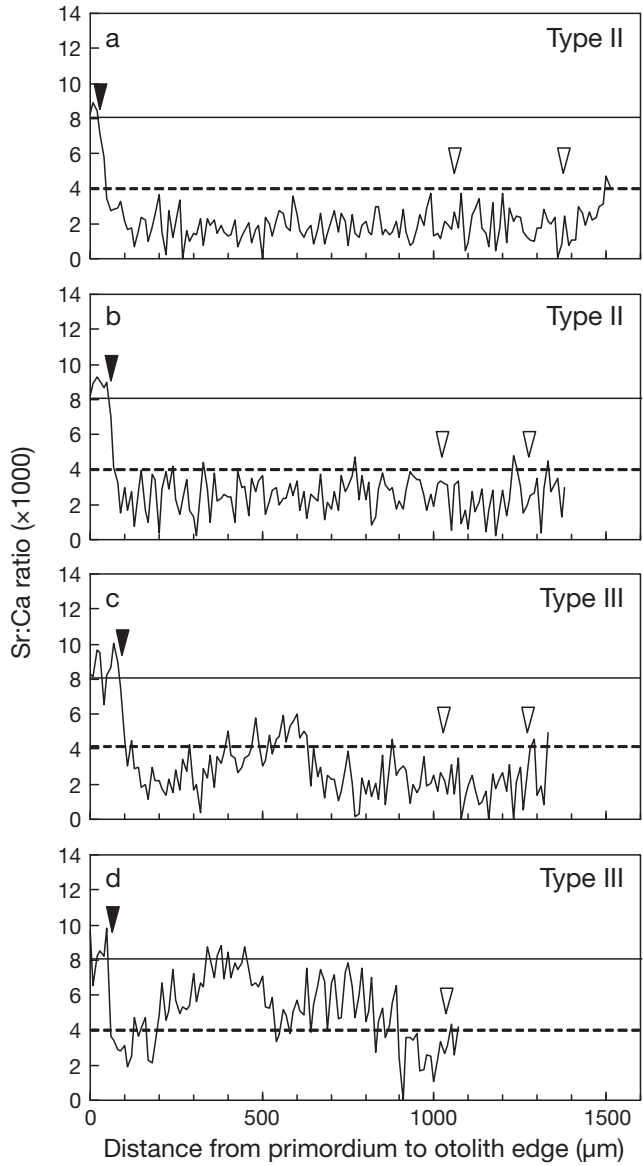


Fig. 5. *Megalops cyprinoides*. Temporal changes in otolith Sr:Ca ratios of young Pacific tarpon collected in the middle reach of Tadu Creek (MT in Fig. 1). (a) 264.1, (b) 252.9, (c) 247.1, and (d) 226.3 mm fork length. (▼) Metamorphosis check; (▽) annual rings. The freshwater–brackishwater boundary (dashed lines) was set at 4×10^{-3} , while the brackish–seawater boundary (solid lines) was 8×10^{-3} . Type I: brackish-water residents; Type II: freshwater residents; Type III: vagrants between brackish and fresh waters

Age-specific habitat selection and migratory behavior

Age 1+ tarpon constituted 9.7% of the total specimens collected in the freshwater environment of Tadu Creek, but no age 1+ tarpon were found offshore (Fig. 7a). One age 2+ tarpon was found offshore (5.3% of the total catch for offshore sampling) but most fishes

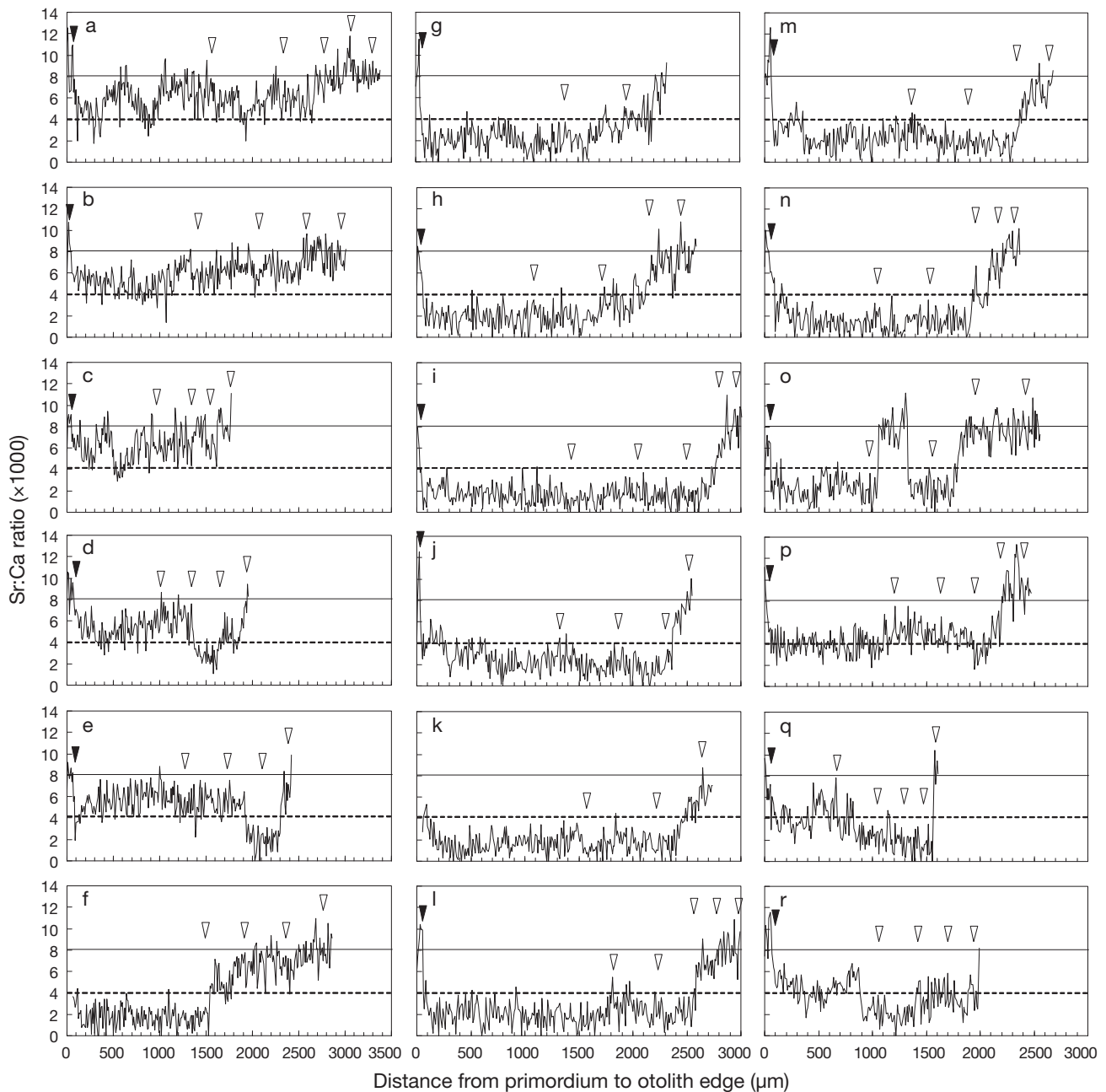


Fig. 6. *Megalops cyprinoides*. Temporal changes in otolith Sr:Ca ratios of sub-adult Pacific tarpon collected in the waters offshore of Tadu Creek. (a) 377.3, (b) 407.2, (c) 364.5, (d) 347.2, (e) 391.9, (f) 419.3, (g) 300.2, (h) 391.2, (i) 378.3, (j) 345.7, (k) 276.1, (l) 435.1, (m) 365.3, (n) 401.8, (o) 349.5, (p) 384.3, (q) 405.1, and (r) 346.7 mm fork length. (▼) Metamorphosis check; (▽) annual rings. The freshwater–brackishwater boundary (dashed lines) was set at 4×10^{-3} , while the brackishwater–seawater boundary (solid lines) was 8×10^{-3}

stayed in the fresh water (66.1% of specimens collected in fresh water) of Tadu Creek. At age 3+, 24.2% of tarpon remained in fresh water while 10.5% moved offshore. All tarpon moved offshore at ages 4+ and 5+. The frequency distributions of age-specific habitat selection differed significantly between fresh and offshore waters (Kolmogorov-Smirnov $D = 0.8421$, $p < 0.001$).

The accumulated frequency of freshwater residents (Type II) was higher (58%) than for brackishwater residents (Type I) (27.2%) and for vagrants (Type III) (14.8%) at age 1+. The accumulated frequencies of Type II and Type I gradually decreased with age until age 3+ but gradually increased with age for Type III. At age 4+ and 5+, all tarpon were Type III (Fig. 7b).

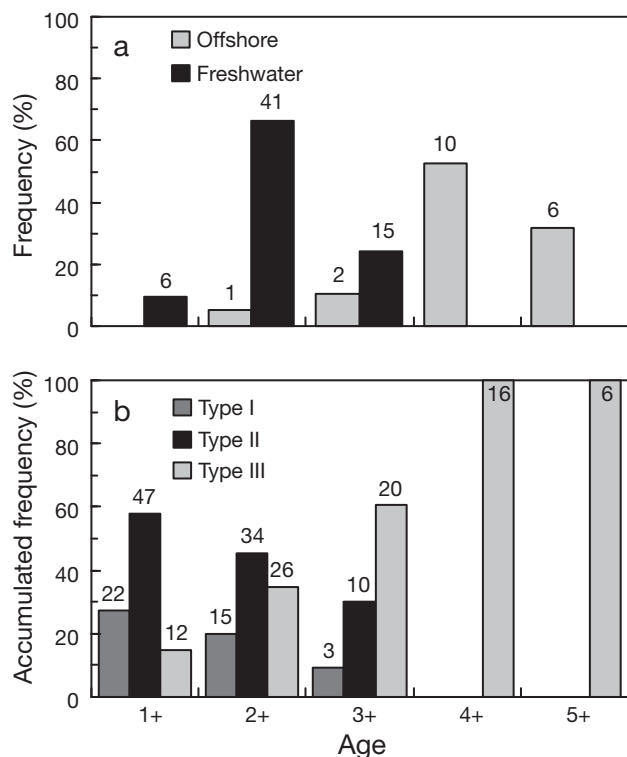


Fig. 7. *Megalops cyprinoides*. (a) Frequency distributions of age-specific habitat use (b) and the accumulated frequencies of age-specific migratory patterns (Types I, II and III refer to Fig. 4). Numbers above bars are sample sizes

DISCUSSION

Migratory history reconstruction from otolith Sr:Ca ratios

Fish movements between marine, estuarine, and freshwater habitats have been reconstructed from temporal changes in otolith Sr:Ca ratios for anguillid eels (Japanese eel *Anguilla japonica*: Tzeng & Tsai 1994, Tzeng et al. 2002a, 2003; European eel *Anguilla anguilla*: Tzeng et al. 1997; American eel *Anguilla rostrata* (Jessop et al. 2002, 2004) striped bass *Morone saxatilis* (Secor & Piccoli 1996) and amphidromous goby *Sicyopterus japonicus* (Shen & Tzeng 2002). The incorporation of Sr into the otolith is a complex biogeochemical process which is influenced by both intrinsic and exogenous factors (Fowler et al. 1995) as well as the crystalline structure of the otolith (Tzeng et al. 2007). Although the ambient temperature may affect the Sr:Ca ratio of the otolith (Townsend et al. 1992, Elsdon & Gillanders 2004), the effect of temperature on otolith Sr:Ca ratios in Pacific tarpon was found to be negligible (Tzeng 1996, Chen et al. 2008). Ambient salinity is the main factor affecting otolith Sr:Ca ratios in reared leptocephali (Chen & Tzeng 2006, Chen et al. 2008). The Sr:Ca ratios used to judge Pacific tarpon migra-

tions between freshwater, brackishwater and offshore environments were similar to those used for other fish species. For example, Jessop et al. (2002, 2004) divided the American eel into freshwater and estuarine residents when otolith Sr:Ca ratios were $<4 \times 10^{-3}$ and $>5 \times 10^{-3}$, with the intermediate values representing a change in habitat. Tzeng et al. (2002a, 2003) used a Sr:Ca ratio of 4×10^{-3} in the otoliths of the Japanese eel as a criterion to distinguish freshwater and seawater contingents. Shiao et al. (2003) also used the upper limit of 4×10^{-3} as a criterion to separate the Japanese eel and the giant mottled eel *Anguilla marmorata* into freshwater, estuarine or marine residents. Kawakami et al. (1998) reported Sr:Ca ratios in Japanese eel elvers that averaged $\sim 4.5 \times 10^{-3}$ in fresh water and 8.3×10^{-3} in seawater. Chang et al. (2004), however, used the 95% CI of the mean Sr:Ca ratio at the estuarine check of the adult mullet otolith (3×10^{-3} and 7×10^{-3}) as the criterion to distinguish habitat change between fresh water, brackish water and offshore high-salinity water for the grey mullet *Mugil cephalus*. The similarities in criteria used for different fishes living in the same environment suggest that plasma ionic homeostasis may occur for different fishes in certain environments. The minor differences observed among the studies may result from differences in analytical methods, sampling sites and species (Jessop et al. 2002).

Facultative migratory behavior and euryhalinity in sub-adult Pacific tarpon

The tarpon, like many other estuarine-dependent marine fishes, recruit to an estuarine nursery habitat during the age 0+ period of their life history, but the migratory behavior of young and sub-adult tarpon is not yet fully understood. After the reconstruction of the migratory environmental history of the Pacific tarpon using Sr:Ca ratios, all 3 migratory types were found in the lower reach of the freshwater stream, but Type I was not found in the middle reach of Tadu Creek. This means that Type I individuals preferred to stay in brackish water, might move to the lower reaches of the freshwater stream, but would not get into the middle reach. In contrast, Type II individuals preferred the freshwater environment, and might stay in either low or middle reaches of the Creek, suggesting higher adaptability to the freshwater environment. Type III individuals had the ability to migrate between brackish and freshwater environments within age 0+, enabling them to select a wider range of habitats. The sub-adult tarpon caught in offshore waters all had higher Sr:Ca ratios at the otolith edge, but their past migratory history shows that they fit the 3 migratory behaviors of the tarpon in the creek. Most tarpon (53%) stayed in a freshwater en-

vironment for 1 to 3 yr, but some tarpon still stayed in a brackishwater environment for 2 to 3 yr before moving offshore or to a freshwater environment, or migrated between freshwater and brackishwater environments. Therefore, the migratory behavior of tarpon is highly variable and facultative. Tarpon tended to stay in fresh water at ages 0+ to 1+ but as age increased, the proportion of fish inhabiting fresh water decreased and no fish at age 4+ (n = 16) or older (n = 6) inhabited fresh water.

Tarpon occupy a high trophic level and are predominantly piscivorous. Atlantic tarpon, for example, prey on mullet juveniles during their migrations along the Caribbean coast from March to July (Catano & Garzon-Ferreira 1994). Pacific tarpon also prey on mullet in both brackish and fresh waters and on milkfish in culture ponds of Taiwan (Tzeng & Yu 1986), suggesting a euryhaline habit.

Where do the mature Pacific tarpon go?

Mature Atlantic tarpon are usually >1000 mm in standard length and around 10 yr old (Crabtree et al. 1997), with 1 female Atlantic tarpon being reported to be 2032 mm in standard length (Wade 1962). Few Pacific tarpon in Taiwan are >600 mm in total length (TL), but a Pacific tarpon of 1500 mm TL was recorded in Bangladesh (Rahman 1989). All tarpon collected in the present study were immature because no obvious gonads were found. The newly recruited leptocephalus had daily ages ranging from 18 to 34 d, suggesting that the spawning ground was nearby. In addition, adult Pacific tarpon may go deeper for spawning just like the Atlantic tarpon (90 to 1400 m) (Wade 1962, Crabtree et al. 1992) and other members of the Superorder Elopomorpha (Tsukamoto et al. 2002). The 19 sub-adults collected offshore from Tadu Creek were estimated to be 2 to 5 yr old based on the examination of annual rings in their otoliths. While our study does not directly answer the question of where mature Pacific tarpon live, the high Sr:Ca ratios in the leptocephalus stage and the spawning behavior of its congeners support the hypothesis of deep-sea spawning in offshore waters.

In conclusion, we found that (1) after metamorphosing from the leptocephalus to the juvenile stage, Pacific tarpon found in Tadu Creek could inhabit fresh and brackish waters or migrate facultatively between these habitats, (2) at age 0+, tarpon preferentially occupy fresh water, (3) tarpon gradually move back to marine waters after 4 yr of age, indicating euryhaline behavior and facultative habitat selection by sub-adults, and (4) the spawning migration of the tarpon is still unknown but the high Sr:Ca ratio during the leptocephalus stage supports the hypothesis of offshore spawning by Pacific tarpon.

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