東京湾内湾に造成された人工砂浜海岸における魚類群集の構造

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Fish assemblage structures on artificial sandy beaches in inner Tokyo Bay, central Japan

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Abstract: Daytime seine net sampling was conducted on three artificial sandy beaches（Inage, Kemigawa and Makuhari）formed on reclaimed land at Mihama, Chiba Prefecture, central Japan, in September and November 2017, and May and July 2018. A total of 1091 individual fishes, representing 19 families and 23 species, were collected throughout the study period. Five species （*Lateolabrax japonicus*, *Platichthys bicoloratus*, *Konosirus punctatus*, *Hypoatherina valenciennei* and *Plecoglossus altivelis altivelis*）were dominant, accounting for 87.4% of all individuals. Almost all of the species collected were represented only by juveniles, suggesting that the artificial sandy beaches were used as an important juvenile habitat by a variety of fishes. Although no differences in total numbers of fish species and individuals, and species composition were found among the three beaches, the mean standard length of fish pooled for each species tended to be smaller on Kemigawa Beach than the other two beaches. This difference may be due to the protected aspect of the former beach, resulting in relatively low wave activity, due to the construction of inwardly-curved groins on either side of the beach.

Keywords: *Artificial sandy beach, Fish assemblage, Juvenile, Tokyo Bay*

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1.　はじめに

　砂浜海岸は，地球上の氷結しない海岸線の三分の二を占めており（MCLACHLAN and DEFEO, 2018），日本列島においても海岸線の多くの部分を占めている（佐野，2017）。砂浜海岸（以下，砂浜）は，一見すると海底環境が単調なため，生物の生息場としては重要でないといわれることが多い。しかし実際には，波浪や堆積物，潮汐などの相互作用により複雑な海底環境が生み出され，これまでに魚類をはじめとする数多くの生物が採集されている（佐野，2017; 須田，2017; MCLACHLAN *et al.*, 2018）。したがって，砂浜は沿岸浅海域の生態系や生物多様性を理解するうえで重要な水域の

1つであるといえる。特に魚類においては，砂浜の無脊椎動物を主要な餌としていることや，成魚と比べ，稚魚が多くみられることなどから，砂浜は魚類の餌場や稚魚の生息場となっている可能性が示唆されている（e.g., LASIAK, 1986; 須田，2002; INOUE *et al.*, 2005; NAKANE *et al.*, 2011; 井上，2017; McLACHLAN and DEFEO, 2018; OLDS *et al.*, 2018）。こうしたことから，砂浜は魚類にとって重要な生息場の1つであると考えられている。

　砂浜を含む浅海の沿岸域は，港湾建設や埋め立てなどによる人工改変を受けやすい場所でもある。特に東京湾の内湾（富津岬と観音崎を結んだ線以北の海域）では，かつて干潟や浅瀬が広がっていたが，1970年代までにそのほとんどが消失した（荒山ほか，2002; 河野ほか，2012）。一方，近年では，失われた海岸環境を取り戻そうとする動きがあり，そのための施策の1つとして人工砂浜が造成されるようになった（菅原，1977）。特に，千葉市美浜区のいなげの浜や検見川の浜，幕張の浜はその良い例であり，これらの人工砂浜は，干潟と浅瀬が完全に消失した埋立地先の海岸部に造成されている（風呂田，1997a）。中でもいなげの浜はわが国初の人工砂浜である（小倉ほか，2010）。しかし，これらの人工砂浜にどのような生物が生息しているのか，とりわけ魚類についてはまだほとんどわかっていないのが現状である。

　さらに，これら3つの人工砂浜のうち，検見川の浜には内側に湾曲した突堤が両端にあるため，いなげの浜や幕張の浜よりは波浪に対して保護的な環境が形成されている可能性がある。例えば，保護的な砂浜では沖合からの波浪が直接には進入できないため，開放的な砂浜よりも波高が低く，波当たりが弱い環境となる（時岡ほか，1972; CLARK, 1997; 青木ほか，2016）。波浪環境は魚類群集の構造に影響を与える要因の1つであるといわれており，波浪の穏やかな環境では遊泳力に乏しい小型魚や稚魚が多く出現することが知られている（NAKANE *et al.*, 2013; TATEMATSU *et al.*, 2014; 荒山・河野，2015）。検見川の浜は，いなげの浜や幕張の浜よりも波浪が穏やかなことが推測されるため，前者の砂浜と後2者の砂浜との間では異なる

魚類群集が形成されている可能性がある。

　そこで本研究では，いなげの浜，検見川の浜，幕張の浜の3つの人工砂浜において魚類を複数の月にわたって採集し，これらの砂浜に出現する魚類群集の構造を明らかとするとともに，砂浜間でその群集構造に違いがあるのかどうかを調べた。また，物理的環境（水質，波浪，底質など）と生物的環境（魚類の餌生物としての無脊椎動物の個体数密度）を調べることで，魚類群集構造と環境特性との関係についても検討した。

2.　材料と方法
2.1　調査地の概要と調査期間

　調査は，千葉市美浜区のいなげの浜（北緯35°36′56″，東経140°03′45″），検見川の浜（北緯35°37′46″，東経140°02′47″），幕張の浜（北緯35°38′19″，東経140°02′07″）の3つの人工砂浜において，2017年9月，11月，2018年5月，7月に実施した（Fig. 1）。いなげの浜は1976年に造成された延長1200 mの人工砂浜である（菅原，1977; 高荷，2002）。この砂浜は沖合3 kmにあった砂を用いて造成されており，砂浜の両端には長さ200 mの直線状の突堤が存在する（菅原，1977）。検見川の浜は1988年に造成された延長1300 mの人工砂浜であり（高荷，2002），造成用の砂には富津と小櫃川河口のものが用いられている（千葉県土木部港湾建設課，1982）。この砂浜の両端には，内側に湾曲した長さ593 mの突堤が，また中央部付近には長さ約200 mのY字状の突堤がある（熊田・小林，2000）。幕張の浜は1979年に造られた延長1820 mの人工砂浜であり，造成には沖合の砂が用いられている（田中，1980）。この砂浜は4基の直線状の突堤によって3分割されており，それぞれの突堤の長さは北側から順に250, 82, 250, 180 mである（田中，1980; 小林ほか，2013）。これら3つの人工砂浜は河川や水路を挟んで隣接しており，本調査域における朔望平均満潮位と干潮位の差は約2 mである（菅原，1977; 田中，1980; 熊田・小林，2000）。
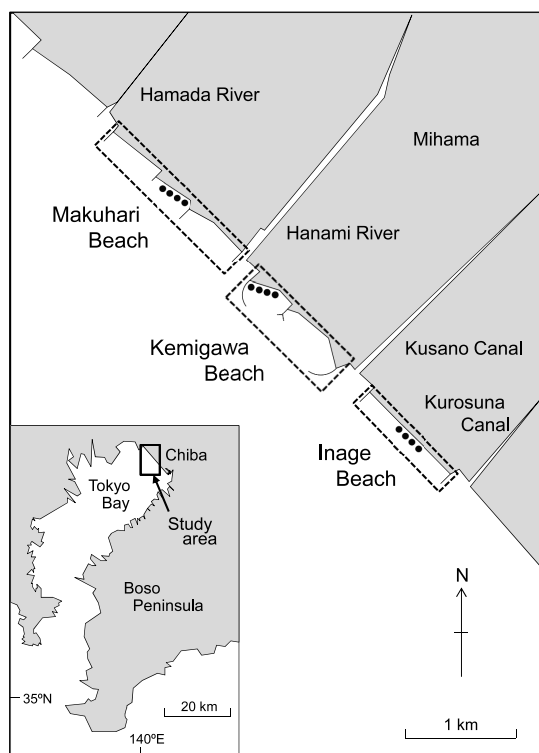
　調査は，それぞれの砂浜において，水深約1 mの場所に，50 m以上の間隔で4定点を設けて行っ

Fig. 1 Map of the study area at Mihama, Chiba Prefecture, central Japan, showing three artificial sandy beaches (Inage, Kemigawa and Makuhari). ●, sampling point.

た（Fig. 1）。各定点において小潮前後の日中に物理的環境，生物的環境，および魚類の調査を同時に実施した。なお，物理的環境である砂浜勾配の測量は，大潮の干潮時に4定点の中央部で行った。

2.2　物理的環境

　各月の各砂浜の4定点において，水質，波浪，底質の調査を行った。また，砂浜勾配の測量は2018年9月に行った。

2.2.1　水質

　多項目水質計 Quanta（HACH 社製）を用いて，水温（℃），塩分，濁度（NTU），溶存酸素量（mg/L）を測定した。測定は各月の各定点で1回とした（$n = 4$/ 砂浜 / 月）。

2.2.2　波浪

　波浪環境の指標として，波高（cm）と波浪周期（s）を測定した。波高は，目盛りの付いたプラスティック製の測定棒を鉛直に立て，測定棒を通過した波の峰と谷の水位（cm）を目視で3分間測定し，峰の最大値と谷の最小値の差を求めることで算出した。波浪周期は，30秒間に測定棒を通過した波の峰の数を計数し，その逆数に30を乗じることで求めた。測定は各月の各定点で1回とした。

2.2.3　底質

　砂の中央粒径値と底質中の有機物含量（以下，強熱減量）を調べた。直径5 cm の円筒形コアサンプラーを海底の表面から深さ約10 cm まで挿入し，底質試料を採取した。試料の採取は各月の各定点で1回とした。採取した試料は100 g を中央粒径値の測定に，30 g を強熱減量の測定に供した。それぞれの分析・測定は以下の手順で行った。

　中央粒径値は，ふるいわけ分析法（日本海洋学会，1986; 土質試験法編集委員会，1990）によって調べた。まず，試料を研究室にて脱塩処理を行い，過酸化水素水を加えて底質中の有機物を分解した後，60 ℃の恒温槽内で十分に乾燥させた。次に，この試料を，目合い 2000, 1000, 500, 250, 125, 63 μm の篩を用いてふるい振とう機 A-3 PRO（FRITSCH 社製）でふるった。ふるいわけ後，それぞれの篩に残った試料を電子天秤で 0.01 g まで秤量し，各粒径サイズの累積重量が 50% となる値を中央粒径値（μm）とした。

　強熱減量の測定は，環境庁水質保全局水質管理課（1988）の底質調査方法の改変法に従った。試料を 60 ℃の恒温槽内で十分に乾燥させた後，恒量化したるつぼに入れ，550 ℃で6時間強熱した。このとき，強熱前後で減少した試料重量の割合として強熱減量(%)を求めた。なお，秤量は 0.001 g 単位で行った。

2.2.4　砂浜勾配

　トータルステーション CS-101F（トプコン社製）

を用いて，満潮時の汀線付近から干潮時の水深1.2 m の地点までの砂浜断面をレベル測量した。測量は，2018 年 9 月に，各砂浜の 4 定点の中央部で 1 回行った（$n = 1$/ 砂浜）。さらに，測量時にラネルとリッジの有無も確認した（須田・南條，2017）。

2.3 生物的環境

各月の各砂浜の 4 定点において，浮遊性，表在性，埋在性の無脊椎動物を採集した。

2.3.1 浮遊性無脊椎動物

濾水計を取り付けたプランクトンネット（口径30 cm，側長 50 cm，網目 100 μm）を汀線と平行方向に 40 m 曳網し，浮遊性無脊椎動物を採集した。曳網は各月の各定点で 1 回とした。採集した浮遊性無脊椎動物はただちに 5% 中性ホルマリン溶液で固定し，研究室に持ち帰った。標本は，プランクトン標本分割器で分割した後，実体顕微鏡下において目のレベルで同定を行い，それぞれの目ごとに個体数を計数した。分割前の個体数は，計数した個体数に分割数をかけることで概算した。この概算値を濾水量で割って，1 m^3 あたりの個体数密度を算出した。

2.3.2 表在性無脊椎動物

ソリネット（幅 50 cm，高さ 10 cm，網目 335 × 335 μm）を汀線と平行方向に 5 m 曳網（曳網面積は 2.5 m^2）して，表在性無脊椎動物を採集した。曳網は各月の各定点で 1 回とした。採集した表在性無脊椎動物はただちに 5% 中性ホルマリン溶液で固定し，研究室に持ち帰った。標本は，実体顕微鏡下において目のレベルで同定を行い，それぞれの目ごとに個体数を計数した。なお，個体数が多かった場合には，計数を行う前に適宜，分割を行った。分割方法および分割前の個体数の概算は，浮遊性無脊椎動物と同様の方法で行った。個体数密度は 1 曳網（2.5 m^2）あたりで求めた。

2.3.3 埋在性無脊椎動物

直径 10 cm の円筒形コアサンプラーを海底の表面から約 15 cm の深さに挿入して，1178 cm^3 の砂を採取した。砂はその場で目合い 1 mm の篩でふるい，埋在性無脊椎動物を採集した。採集は各月の各定点で 1 回とした。採集した埋在性無脊椎動物はただちに 5% 中性ホルマリン溶液で固定し，研究室において実体顕微鏡下で綱のレベルまで同定した。個体数の計数は綱ごとに行い，密度は 1 コア（1178 cm^3）あたりの個体数で示した。

2.4 魚類

各月の各砂浜の 4 定点において，小型地曳網（長さ 16 m，高さ 1.5 m，袖網の目合い 6 mm，袋網の目合い 5 mm）を用いて魚類を採集した。地曳網は，間口を 6 m に保ちながら，汀線と平行方向に 50 m 曳網（曳網面積は 300 m^2）した。曳網は各月の各定点で 1 回とした。採集した魚類は現場でただちに 10% 中性ホルマリン溶液で固定し，研究室に持ち帰った。標本は，主に中坊（2013）や沖山（2014）に従って種の同定を行い，各種の個体数を計数した。ただし，イシガレイ *Platichthys bicoloratus* とクサフグ *Takifugu alboplumbeus* の学名はそれぞれ尼岡（2016）と MATSUURA（2017）に従った。個体数密度は 1 曳網（300 m^2）あたりの値とした。また，デジタルノギスを用いて，各個体の標準体長（以下，体長）を 0.1 mm 単位で計測した。

採集された魚類は，体長や形態学的特徴，既存の知見（中村，1969; 落合・田中，1986; 益田ほか，1988; 中坊，2013; 沖山，2014）を参考にしながら，各個体の発育段階に基づき仔魚，稚魚，成魚の 3 つに区分した。さらに，食性を調べた既往研究の結果に従って，各魚種を浮遊性無脊椎動物食，アミ類食，等脚類食，多毛類食，デトリタス食の 5 グループに分類した（KANOU *et al.*, 2004; INOUE *et al.*, 2005; NAKANE *et al.*, 2011; MIKAMI *et al.*, 2012; TATEMATSU *et al.*, 2014）。なお，既往研究によって食性を決めることができなかった種については，NAKANE *et al.*（2011）の方法に従って消化管内容物を調べることで食性を明らかにした。

2.5 解析方法

物理的環境の各項目，浮遊性，表在性，埋在性無脊椎動物の個体数，魚類の種数，総個体数および体長について，月間（2017 年 9，11 月，2018 年 5，7 月）および砂浜間（いなげの浜，検見川の浜，幕張の浜）で違いがみられるかどうかを調べるために，一般化線形モデル（GLM）に基づく尤度比検定を行った。目的変数は，物理的環境の各項目，無脊椎動物の個体数，魚類の種数，総個体数および体長とし，説明変数は月，砂浜およびそれらの交互作用とした。さらに，優占した魚種の体長組成について砂浜間での違いを調べるために，2018 年 5 月に採集されたスズキ *Lateolabrax japonicus* とイシガレイを用いて尤度比検定を行った。目的変数は各魚種の体長とし，説明変数は砂浜とした。これらのモデルの誤差分布は，物理的環境の各項目および魚類の標準体長については正規分布，魚類の種数についてはポアソン分布，無脊椎動物および魚類の個体数については負の二項分布とした。リンク関数には，正規分布においては identity，ポアソン分布および負の二項分布においては log を指定した。月間あるいは砂浜間で有意差がみられた場合には，多重比較検定（HOLM-BONFERRONI test）を用いて，どの月間あるいは砂浜間で差があるのかを検定した。月と砂浜の交互作用が存在した場合には，各砂浜における月間での有意差の有無と，各月における砂浜間での有意差の有無を尤度比検定によって調べた。月間あるいは砂浜間に有意差が存在した場合には，多重比較検定により，どの月間あるいは砂浜間に有意差が存在したのかを検定した。

魚類の種組成について，月間および砂浜間でどの程度異なるのかを明らかにするために，各月の各砂浜で採集した各種の個体数に基づき類似度を求め，クラスター分析を行った。類似度には BRAY-CURTIS 類似度（*BC*）を，クラスター連結には群平均法を用いた（小林，1995; 土居・岡村，2011）。

$$BC = 1 - \sum_{i=1}^{n} |X_{iA} - X_{iB}| / \sum_{i=1}^{n} (X_{iA} + X_{iB})$$

ここでは，X_{iA} と X_{iB} はそれぞれある月の砂浜 A と B における種 i の個体数を表し，種組成が完全に異なる場合は $BC = 0$，まったく同じ場合には $BC = 1$ となる。なお，個体数が種によって大きく異なるとき，類似度指数は個体数の多い種の影響を受けやすい。このため，本解析においては個体数の少ない種の貢献度を高めるために，各種の個体数を対数変換 [log（$x + 1$）] した。

以上の解析には，統計ソフト R 3.4.0 を用いた。また，それぞれの検定における有意水準は 5% とした。

3. 結果

3.1 物理的環境

3.1.1 水質

各月の各砂浜における水温，塩分，濁度，溶存酸素量の結果を Fig. 2 に示した。これらの各項目について月間および砂浜間で違いがみられるかどうかを調べるために，GLM を用いて尤度比検定を行ったところ，すべての項目において月と砂浜の交互作用がみられた（Table 1）。そこで，これらの各項目について各砂浜における月間での有意差の有無と，各月における砂浜間での有意差の有無を尤度比検定によって調べた（Table 1）。

水温は，すべての砂浜において月間での有意差がみられた。いなげの浜では 7 月，9 月，5 月，11 月の順に，また検見川の浜では 7 月，9 月，11 月，5 月の順に高かった。幕張の浜では 7 月＞9 月＞11 月 = 5 月となった。各月における砂浜間での違いについては，7 月を除くと，各月で有意差がみられた。9 月では検見川や幕張の浜がいなげの浜よりも高く，11 月では検見川，幕張，いなげの浜の順に高かった。一方，5 月ではいなげの浜が検見川や幕張の浜よりも高かった。しかし，いずれの月においても砂浜間の差はわずかで，最大でも 1.4℃ であった。

塩分は，すべての砂浜において月間での有意差がみられた。いなげや検見川の浜では 5 月，9 月，11 月，7 月の順に高く，幕張の浜では 5 月＞9 月 = 11 月＞7 月であった。各月における砂浜間での違いについては，すべての月で有意差がみられ
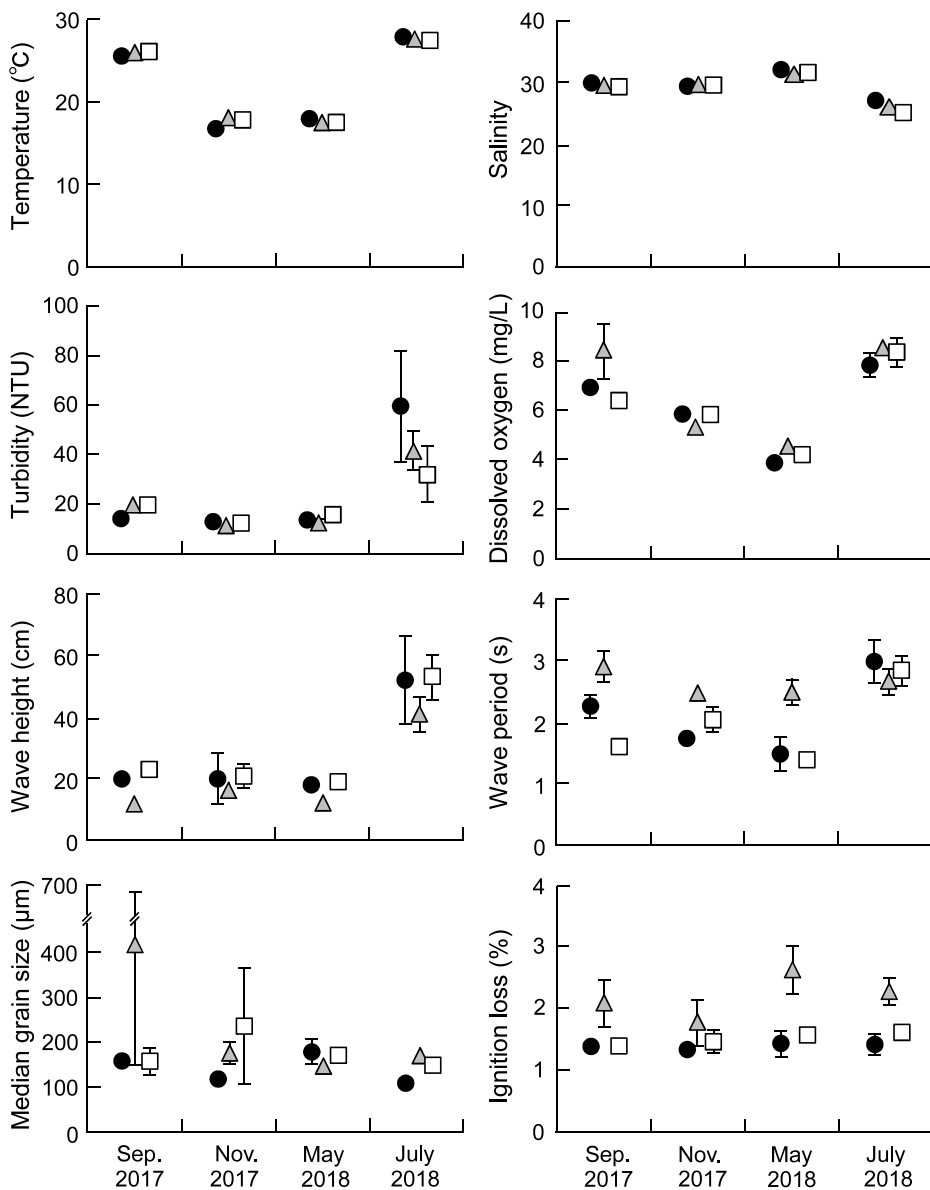
Fig. 2 Physical environmental factors（water temperature, salinity, turbidity, dissolved oxygen, wave height, wave period, median grain size and organic content, indicated by ignition loss）on Inage Beach（●）, Kemigawa Beach（▲）and Makuhari Beach（□）in September and November 2017, and May and July 2018. Data include means ± standard deviations（*n* = 4）.

た。9月ではいなげの浜で高く，幕張の浜で低かった。11月では検見川や幕張の浜はいなげの浜よりも高かった。5月においてはいなげ，幕張，検見川の浜の順に高く，7月ではいなげ，検見川，幕張の浜の順に高かった。しかし，いずれの月においても砂浜間の差はわずかで，最大でも2.2の

差であった。

　濁度は，すべての砂浜において月間での有意差がみられ，いずれの砂浜においても7月が他の月よりも高かった。各月の砂浜間での違いは，11月を除くと，各月で有意差がみられた。9月においては検見川や幕張の浜がいなげの浜よりも高く，5月では幕張の浜が検見川の浜よりも高かった。一方，7月では多重比較検定で差が検出されなかったが，Fig. 2をみると，いなげの浜で高く，検見川や幕張の浜で低い傾向がみられた。

　溶存酸素量についても，すべての砂浜において月間で有意差がみられた。いなげの浜では7月，9月，11月，5月の順に高く，検見川と幕張の浜ではそれぞれ9月＝7月＞11月＝5月，7月＞9月＝11月＞5月であった。各月の砂浜間での違いは，7月を除くと，各月で有意差がみられ，9月においては検見川の浜がいなげや幕張の浜よりも高かった。一方，11月ではいなげや幕張の浜で高く，5月では検見川の浜がいなげの浜よりも高かった。

3.1.2　波浪

　各月の各砂浜における波高と波浪周期の結果をFig. 2に示した。波浪周期では月と砂浜の交互作用がみられたため，各砂浜における月間での有意差と各月における砂浜間での有意差を調べた（Table 1）。

　波高は月間での有意差がみられ，7月は他の月よりも高かった。また，砂浜間でも有意差が認められたが，多重比較検定では差が検出されなかった。しかし，Fig. 2をみると，いなげや幕張の浜は検見川の浜よりも高い傾向にあった。

　波浪周期は，すべての砂浜において月間での有意差がみられ，いなげの浜では7月＞9月＞11月＝5月であった。検見川の浜においては，尤度比検定で月間の有意差が認められたが，多重比較検定では差が検出されなかった。しかし，9月は他の月よりもやや長い傾向にあった（Fig. 2）。幕張の浜では7月＞11月＞9月＝5月となった。各月における砂浜間での違いについては，7月を除くと，各月で有意差がみられた。9月では検見川，いなげ，幕張の浜の順で，また11月では検見川，幕張，いなげの浜の順で長かった。5月においては，検見川の浜でいなげや幕張の浜よりも長かった。

3.1.3　底質

　各月の各砂浜における中央粒径値と強熱減量の結果をFig. 2に示した。尤度比検定の結果，どちらの項目でも月と砂浜の交互作用がみられた（Table 1）。

　中央粒径値は，いなげと検見川の浜において月間での有意差がみられ，前者の浜では5月＝9月＞7月＝11月であった。一方，後者の浜においては，9月が7月よりも大きかった。各月の砂浜間での違いについては，9月と7月に有意差がみられた。9月では多重比較検定で差が検出されなかったが，検見川の浜がいなげや幕張の浜よりも大きい傾向にあった（Fig. 2）。7月では検見川や幕張の浜がいなげの浜よりも大きかった。

　強熱減量については，検見川と幕張の浜において月間での有意差が認められ，どちらの浜も5月と7月が他の月よりも高い傾向にあった。各月の砂浜間の違いについては，すべての調査月において有意差がみられた。9月，11月，5月においては検見川の浜でいなげや幕張の浜よりも高く，7月では検見川，幕張，いなげの浜の順で高かった。

3.1.4　砂浜勾配

　9月に測量した各砂浜の勾配は，いなげの浜で1/27，検見川の浜と幕張の浜で1/24であった。勾配はいなげの浜でやや緩やかであったものの，砂浜間で大きな違いはみられなかった。また，どの砂浜においても，満潮時の汀線付近から干潮時の水深1.2 mの地点までに，幅5-15 m程度のラネルとリッジがそれぞれ1列存在した。

3.2　生物的環境
3.2.1　浮遊性無脊椎動物

　採集された浮遊性無脊椎動物は主にカラヌス類やキクロプス類であった。各月の各砂浜における1 m^3 あたりの浮遊性無脊椎動物の総個体数をFig.

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Table 1. Results of likelihood-ratio（LR）tests examining the effects of month and beach on physical environmental factors using a generalized linear model（GLM）.

	df	LRx^2	p	HBT
Water temperature				
Month	3	24077.7	<0.001	
Beach	2	12.6	<0.01	
Month×Beach	6	101.8	<0.001	
Month in IN	3	19500.0	<0.001	Jul>Sep>May>Nov
Month in KM	3	8636.8	<0.001	Jul>Sep>Nov>May
Month in MK	3	4725.9	<0.001	Jul>Sep>Nov=May
Beach in Sep.	2	23.9	<0.001	KM=MK>IN
Beach in Nov.	2	506.4	<0.001	KM>MK>IN
Beach in May	2	15.9	<0.001	IN>KM=MK
Beach in July	2	4.6	0.102	
Salinity				
Month	3	8462.3	<0.001	
Beach	2	139.1	<0.001	
Month×Beach	6	225.2	<0.001	
Month in IN	3	2022.3	<0.001	May>Sep>Nov>Jul
Month in KM	3	22520.0	<0.001	May>Sep>Nov>Jul
Month in MK	3	2080.1	<0.001	May>Sep>Nov>Jul
Beach in Sep.	2	23.9	<0.001	IN>MK
Beach in Nov.	2	221.7	<0.001	KM=MK>IN
Beach in May	2	102.4	<0.001	IN>MK>KM
Beach in July	2	190.7	<0.001	IN>KM>MK
Turbidity				
Month	3	135.2	<0.001	
Beach	2	4.2	0.122	
Month×Beach	6	22.7	<0.001	
Month in IN	3	48.7	<0.001	Jul>Sep=Nov=May
Month in KM	3	138.7	<0.001	Jul>Sep=Nov=May
Month in MK	3	25.0	<0.001	Jul>Sep=Nov=May
Beach in Sep.	2	14.3	<0.001	KM=MK>IN
Beach in Nov.	2	3.1	0.216	
Beach in May	2	13.6	<0.01	MK>KM
Beach in July	2	6.6	<0.05	—
Dissolved oxygen				
Month	3	619.7	<0.001	
Beach	2	16.7	<0.001	
Month×Beach	6	46.0	<0.001	
Month in IN	3	350.5	<0.001	Jul>Sep>Nov>May
Month in KM	3	163.6	<0.001	Sep=Jul>Nov=May
Month in MK	3	263.6	<0.001	Jul>Sep>Nov>May
Beach in Sep.	2	19.6	<0.001	KM>IN=MK
Beach in Nov.	2	40.9	<0.001	IN=MK>KM
Beach in May	2	11.8	<0.01	KM>IN
Beach in July	2	5.7	0.058	
Wave height				
Month	3	266.9	<0.001	Jul>Sep=Nov=May
Beach	2	21.5	<0.001	—
Month×Beach	6	2.8	0.828	

Wave period				
Month	3	158.6	<0.001	
Beach	2	89.7	<0.001	
Month×Beach	6	88.2	<0.001	
Month in IN	3	90.5	<0.001	Jul>Sep>Nov=May
Month in KM	3	12.0	<0.01	—
Month in MK	3	154.1	<0.001	Jul>Nov>Sep=May
Beach in Sep.	2	100.5	<0.001	KM>IN>MK
Beach in Nov.	2	62.3	<0.001	KM>MK>IN
Beach in May	2	62.8	<0.001	KM>IN=MK
Beach in July	2	3.0	0.220	
Median grain size				
Month	3	8.9	<0.05	
Beach	2	7.8	<0.05	
Month×Beach	6	20.3	<0.01	
Month in IN	3	56.4	<0.001	May=Sep>Jul=Nov
Month in KM	3	10.5	<0.05	Sep>May
Month in MK	3	4.1	0.253	
Beach in Sep.	2	7.3	<0.05	—
Beach in Nov.	2	4.8	0.089	
Beach in May	2	5.9	0.052	
Beach in July	2	36.0	<0.001	KM=MK>IN
Ignition loss				
Month	3	52.4	<0.001	
Beach	2	336.4	<0.001	
Month×Beach	6	46.2	<0.001	
Month in IN	3	3.6	0.312	
Month in KM	3	39.1	<0.001	May>Sep=Nov, Jul>Nov
Month in MK	3	22.5	<0.001	Jul>Sep=Nov, May>Sep
Beach in Sep.	2	67.7	<0.001	KM>IN=MK
Beach in Nov.	2	19.8	<0.001	KM>IN=MK
Beach in May	2	150.1	<0.001	KM>IN=MK
Beach in July	2	180.3	<0.001	KM>MK>IN

Holm–Bonferroni test (HBT) was conducted when the GLM and LR test results indicated significant effects.

—, The HBT results indicated no significant differences among months or beaches.

IN, Inage Beach; KM, Kemigawa Beach; MK, Makuhari Beach.

3 に示した。尤度比検定の結果，月と砂浜の間に交互作用が存在した（Table 2）。

　総個体数は，すべての砂浜において月間での有意差がみられた。いなげや幕張の浜では 9 月が他の月よりも多く，同様の傾向は検見川の浜でもみられた。また，7 月を除くと，各月の砂浜間でも有意差がみられ，9 月ではいなげの浜が検見川や幕張の浜よりも多かった。11 月と 5 月においては多重比較検定で差が検出されなかったが，11 月では検見川の浜で多く，幕張の浜で少ない傾向にあった（Fig. 3）。一方，5 月ではいなげの浜で多く，検見川の浜で少ない傾向となった。

3.2.2　表在性無脊椎動物

　表在性無脊椎動物で優占していたのはアミ類であった。各月の各砂浜における 1 曳網（2.5 m^2）あたりの表在性無脊椎動物の総個体数とアミ類の個体数を Fig. 3 に，また尤度比検定の結果を Table 2 に示した。いずれの項目においても月と砂浜の交互作用が認められた。

　総個体数は，すべての砂浜において月間での有意差がみられた。いなげの浜では 5 月が 9 月よりも多く，検見川や幕張の浜でも 5 月は他の月よりも多かった。各月における砂浜間での違いについては，5 月を除く各月において有意差が認められ

Table 2. Results of LR tests examining the effects of month and beach on the abundances of zooplankton（total）, epifaunal invertebrates （total and mysids） and infaunal invertebrates （total and poly-chaetes） using a GLM.

	df	LRx^2	p	HBT
Total zooplankton				
Month	3	165.6	<0.001	
Beach	2	17.8	<0.001	
Month×Beach	6	22.6	<0.001	
Month in IN	3	69.5	<0.001	Sep>Nov=May=Jul
Month in KM	3	38.5	<0.001	Sep>Nov=May, Jul>May
Month in MK	3	73.7	<0.001	Sep>Nov=May=Jul
Beach in Sep.	2	36.7	<0.001	IN>KM=MK
Beach in Nov.	2	7.7	<0.05	―
Beach in May	2	7.7	<0.05	―
Beach in July	2	1.8	0.416	
Total epifaunal invertebrates				
Month	3	279.7	<0.001	
Beach	2	11.0	<0.01	
Month×Beach	6	31.2	<0.001	
Month in IN	3	68.2	<0.001	May>Sep
Month in KM	3	50.5	<0.001	May>Sep=Nov=Jul
Month in MK	3	454.4	<0.001	May>Sep=Nov=Jul
Beach in Sep.	2	46.7	<0.001	KM>IN=MK
Beach in Nov.	2	8.1	<0.05	―
Beach in May	2	5.2	0.074	
Beach in July	2	25.9	<0.001	KM>MK
Mysids (epifaunal)				
Month	3	1089.7	<0.001	
Beach	2	6.2	<0.05	
Month×Beach	6	36.6	<0.001	
Month in IN	3	741.2	<0.001	May>Sep=Nov=Jul
Month in KM	3	102.3	<0.001	May>Sep=Nov=Jul
Month in MK	3	275.5	<0.001	May>Sep=Nov=Jul
Beach in Sep.	2	0.7	0.701	
Beach in Nov.	2	19.4	<0.001	MK>KM
Beach in May	2	5.0	0.083	
Beach in July	2	41.5	<0.001	KM>IN=MK
Total infaunal invertebrates				
Month	3	25.0	<0.001	Jul>May
Beach	2	14.0	<0.001	KM>IN=MK
Month×Beach	6	12.4	0.053	
Polychaetes (infaunal)				
Month	3	31.2	<0.001	
Beach	2	13.6	<0.01	
Month×Beach	6	14.4	<0.05	
Month in IN	3	13.4	<0.01	―
Month in KM	3	18.9	<0.001	―
Month in MK	3	14.5	<0.01	―
Beach in Sep.	2	1.1	0.572	
Beach in Nov.	2	9.2	<0.01	―
Beach in May	2	16.2	<0.001	KM>IN=MK
Beach in July	2	7.2	<0.05	―

For abbreviations, see Table 1.
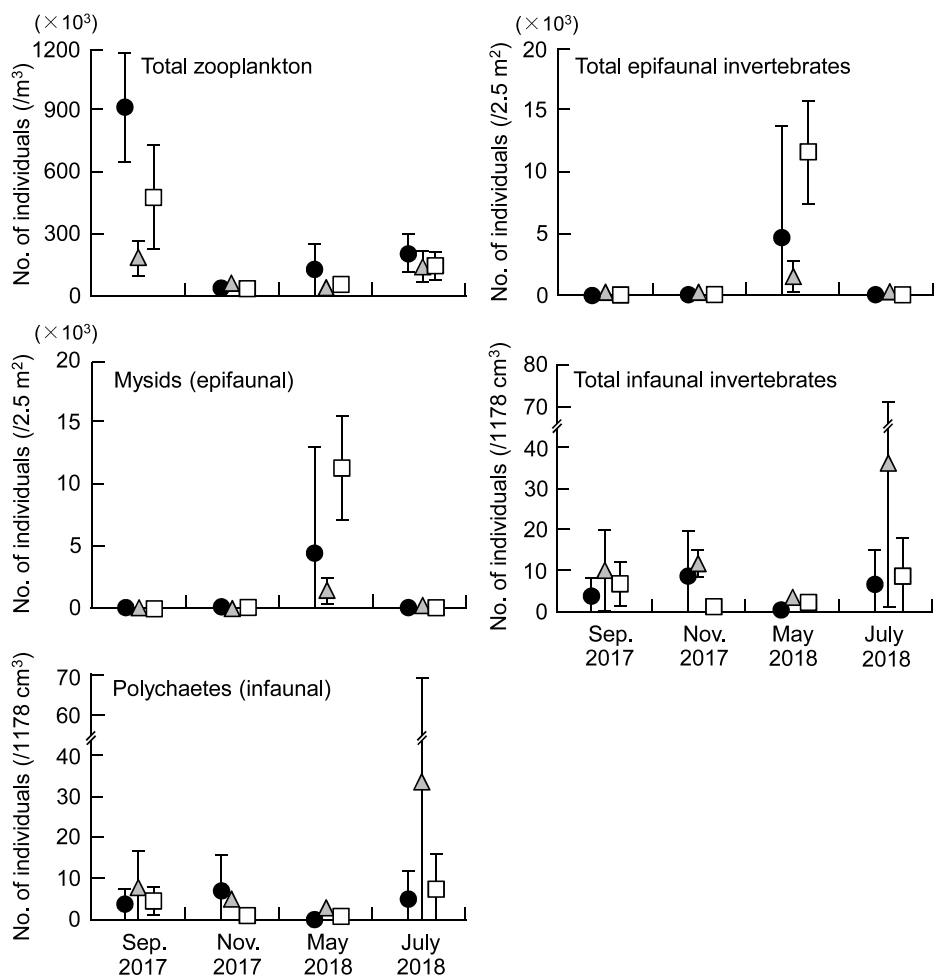HBT was conducted when the GLM and LR test results indicated significant effects.

Fig. 3 Mean individual numbers（± standard deviations, *n* = 4）of zooplankton（total）per m^3, epifaunal invertebrates（total and mysids）per 2.5 m^2 and infaunal invertebrates（total and polychaetes）per 1178 cm^3, collected by plankton net, sledge net and core sampler, respectively, on Inage Beach（●）, Kemigawa Beach（△）and Makuhari Beach（□）in September and November 2017, and May and July, 2018.

た。9 月では検見川の浜でいなげや幕張の浜より
も多く，7 月では検見川の浜が幕張の浜よりも多
かった。11 月は多重比較検定で有意差が検出さ
れなかったが，検見川の浜でいなげや幕張の浜よ
りもわずかに多い傾向がみられた（Fig. 3）。5 月
は，統計的に有意ではなかったが（*p* = 0.074），
Fig. 3 をみると幕張の浜で多い傾向にあった。
　アミ類の個体数についても，すべての砂浜にお

いて月間での有意差が認められ，どの砂浜でも 5
月は他の月よりも多かった。各月の砂浜間での違
いは，11 月と 7 月に有意差がみられた。11 月で
は幕張の浜が検見川の浜よりも多く，7 月では検
見川の浜がいなげや幕張の浜よりも多かった。ま
た，統計的には有意でなかったが（*p* = 0.083），5
月においては幕張の浜で多い傾向がみられた
（Fig. 3）。

3.2.3 埋在性無脊椎動物

埋在性無脊椎動物で優占していたのは多毛類であった。各月の各砂浜における 1 コア（1178 m^3）あたりの埋在性無脊椎動物の総個体数と多毛類の個体数を Fig. 3 に示した。多毛類の個体数については，月と砂浜の間で交互作用がみられた（Table 2）。

総個体数は月間での有意差がみられ，7 月は 5 月よりも多かった。また，砂浜間でも有意差が存在し，検見川の浜はいなげや幕張の浜よりも多かった。

多毛類の個体数では，各砂浜における月間での有意差が認められたが，いずれの砂浜においても多重比較検定で差が検出されなかった。しかし，Fig. 3 をみると，いなげの浜では 11 月にやや多く，検見川や幕張の浜では 7 月に多い傾向が認められた。各月の砂浜間では，9 月を除く各月において有意差がみられたが，11 月と 7 月においては多重比較検定で差が検出されなかった。しかし，11 月ではいなげの浜で，また 7 月では検見川の浜で多い傾向がみられた（Fig. 3）。5 月においては検見川の浜がいなげや幕張の浜よりも多かった。

3.3 魚類群集の構造
3.3.1 採集された魚類

各月の各砂浜で採集された各魚種の個体数，体長，発育段階，食性を Table 3 に示した。調査期間を通して 3 つの砂浜で採集された魚類は，稚魚を中心とした合計 19 科 23 種 1091 個体であった。月ごとにみると，9 月は 7 種 97 個体，11 月は 5 種 9 個体，5 月は 10 種 791 個体，7 月は 10 種 194 個体であった。個体数の多かった魚種は，スズキ（508 個体），イシガレイ（183 個体），コノシロ *Konosirus punctatus*（149 個体），トウゴロウイワシ *Hypoatherina valenciennei*（63 個体），アユ *Plecoglossus altivelis altivelis*（51 個体）の 5 種であり，これらで全体の 87.4% を占めた。これらの優占種はすべて稚魚であり，特定の月や砂浜で多く採集された。スズキは 5 月の幕張の浜，イシガレイとアユは 5 月の検見川の浜，コノシロは 7 月の検見川の浜，トウゴロウイワシは 9 月のいなげ

の浜で多かった。

3.3.2 種数と総個体数

各月の各砂浜における 1 曳網（300 m^2）あたりの種数と総個体数を Fig. 4 に，また尤度比検定の結果を Table 4 に示した。総個体数については月と砂浜の交互作用がみられた。

種数は月間での有意差がみられ，5 月 = 7 月 ＞ 9 月 = 11 月であった。一方，砂浜間では有意差があるとはいえなかった。総個体数は，すべての砂浜で月間の有意差がみられ，検見川の浜においては 5 月 = 7 月 ＞ 9 月 = 11 月，幕張の浜では 5 月 ＞ 9 月 = 7 月 ＞ 11 月であった。いなげの浜では多重比較検定で差が検出されなかったが，9 月が他の月よりもやや多い傾向にあった（Fig. 4）。各月の砂浜間での有意差は，5 月と 7 月にみられた。5 月では幕張の浜がいなげの浜よりも多く，7 月では検見川の浜がいなげや幕張の浜よりも多かった。

3.3.3 種組成

各月の各砂浜で採集した各魚種の個体数に基づき類似度を求め，クラスター分析を行ったところ，類似度 0.2 で 6 つのグループに分かれた（Fig. 5）。これらの各グループをみると，魚類の種組成は 11 月を除き，月ごとに類似していた。また，各月における砂浜間の類似パターンは月ごとに異なっており，調査期間を通してみられた一定の傾向はなかった。

3.3.4 体長

各月の各砂浜で採集された全個体の体長組成を Fig. 6 に示した。尤度比検定の結果，月と砂浜の間に交互作用が存在した（Table 5）。

全個体の体長は，すべての砂浜において月間で有意差がみられた。いなげの浜では 11 月が他の月よりも大きく，同様の傾向は検見川の浜でもみられた。一方，幕張の浜では 9 月と 7 月が 5 月よりも大きかった。各月の砂浜間での違いについては，11 月を除いた各月で有意差がみられた。9 月や 7 月では幕張の浜でいなげや検見川の浜よりも

Table 3. Number of individuals, size ranges in standard length (SL), developmental stages (DS) and feeding habits (FH) of fish species caught by seine net on artificial sandy beaches (Inage, Kemigawa and Makuhari) in each month (September and November 2017, and May and July 2018).

Family	Species	SL (mm)	DS	FH	September 2017			November 2017			May 2018			July 2018			Total
					IN	KM	MK	IN	KM	MK	IN	KM	MK	IN	KM	MK	
Clupeidae	*Sardinella zunasi*	29–91	L–A	Zo			6		1		7				4		18
	Konosirus punctatus	27–127	J	De				5			1				143		149
Engraulidae	*Engraulis japonica*	29–94	L–A	Zo	1	3	3										7
Cyprinidae	*Tribolodon brandtii*	151	J	Po					1								1
Osmeridae	*Hypomesus nipponensis*	56	J	Zo					1								1
Plecoglossidae	*Plecoglossus altivelis altivelis*	33–49	J	Zo								51					51
Mugilidae	*Mugil cephalus cephalus*	26–36	J	Zo								24	2				26
Atherinidae	*Hypoatherina valenciennei*	32–67	J	Zo	48		15										63
Triglidae	*Chelidonichthys spinosus*	13–33	J	My								13	1				14
Platycephalidae	*Platycephalus* sp. 2	31–153	L–A	Po, My	1	2	1					1					5
Lateolabracidae	*Lateolabrax japonicus*	26–84	J	My								13	484	3	1	7	508
Sparidae	*Acanthopagrus schlegelii*	28–51	J	My											1	2	3
Teraponidae	*Terapon jarbua*	32	J	Is	1												1
Oplegnathidae	*Oplegnathus fasciatus*	18–29	J	Zo										2	6	1	9
	Oplegnathus punctatus	18–35	J	Zo											3		3
Kyphosidae	*Kyphosus vaigiensis*	23	J	Zo										1			1
Gobiidae	*Gymnogobius urotaenia*	20–23	J	Zo								1	2	1			4
	Acanthogobius flavimanus	29–105	J	Po	2							1		6	1	8	18
	Favonigobius gymnauchen	32	J	Is					1								1
Pleuronectidae	*Platichthys bicoloratus*	23–78	J	Po							16	150	15			2	183
Triacanthidae	*Triacanthus biaculeatus*	25–66	J	Po		5	9										14
Monacanthidae	*Stephanolepis cirrhifer*	12, 15	J	Zo									1	1			2
Tetraodontidae	*Takifugu alboplumbeus*	76–114	A	My							8			1			9
Number of species					5	3	5	1	4	0	4	8	6	7	7	5	23
Total number of individuals					53	10	34	5	4	0	32	254	505	15	159	20	1091

Data pooled for four replicate sweeps on each beach.

IN, Inage Beach; KM, Kemigawa Beach; MK, Makuhari Beach.

DS: L, larvae; J, juveniles; A, adults.

FH: De, detritus feeders; Is, isopod feeders; My, mysid feeders; Po, polychaete feeders; Zo, zooplankton feeders.
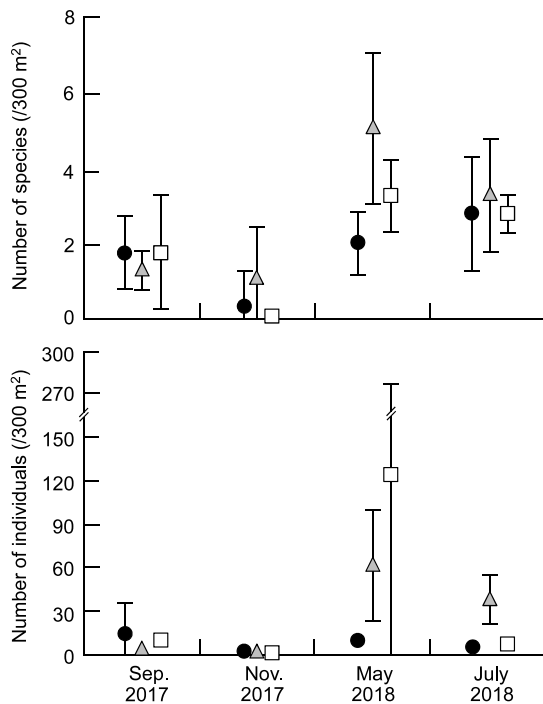
La mer 57, 2019

Fig. 4 Mean numbers（± standard deviations, *n* = 4）of fish species and individuals per 300 m² collected by seine net on Inage Beach（●）, Kemigawa Beach（△）and Makuhari Beach（□）in September and November 2017, and May and July, 2018.

大きく，5 月ではいなげ，幕張，検見川の浜の順に大きかった。

　5 月に採集された優占種のスズキとイシガレイの体長組成を Fig. 7 に示した。両種の体長はそれぞれ砂浜間で有意に異なり，スズキは幕張の浜で検見川の浜よりも大きく，イシガレイはいなげ，幕張，検見川の浜の順に大きかった（Table 5）。

4．考察
4.1　物理的環境
　調査した物理的環境項目のうち，月間の違い（すなわち季節変化）が 3 つの砂浜（いなげの浜，検見川の浜，幕張の浜）において同様のパターンでみられたのは，水温，塩分，濁度，溶存酸素量，波高であった。

　東京湾では，水温と気温の季節変化がほぼ一致しており，夏に高く，冬に低くなることが知られている（風呂田，1997b; 東京湾海洋環境研究委員会，2011）。本研究においても同様の傾向がみられ，水温は 9 月，7 月に高く，11 月，5 月に低かった。

　東京湾の湾奥では，夏の高温期に塩分の低下が著しいことが報告されている（風呂田，1997b; 東京湾海洋環境研究委員会，2011）。本研究でも同様に，塩分は 5 月に高く，7 月で低かった。これは，湾奥に流入する淡水供給量が夏に多くなることが影響していると考えられている（東京湾海洋環境研究委員会，2011）。さらに，この塩分低下は，水塊構造や季節風の方向と深い関係にあるといわれている。風呂田（1997b）によると，夏に湾内で成層が形成され，さらに湾口から湾奥へ向かう季節風（南風）が卓越すると，塩分の低い表層水が湾奥に吹き寄せられるため，塩分低下が助長されるという。

　また，塩分と同様に，本研究でみられた濁度と波高の季節変化も夏の季節風の影響を受けて生じた変化であると推察される。両項目は 7 月において他の月よりも顕著に高かった。これは，夏の季節風によって湾口から吹き寄せられた波が湾奥で高くなるとともに，海底がその波によって撹乱され，濁度が高くなったものと考えられる。

　東京湾内湾の表層域では，溶存酸素量は夏に高くなり，冬に低くなることが報告されている（石井・大畑，2010）。この現象は，植物プランクトンの光合成による酸素発生量を反映したものといわれている。本研究においても概ね同様の傾向を示し，溶存酸素量は 7 月で最も多かった。

　一方，砂浜間での違いが調査期間を通して同様にみられた項目は，波高と強熱減量であった。波高は検見川の浜で他の砂浜よりも低く，逆に強熱減量は検見川の浜で高い傾向を示した。波高が検見川の浜で低いという結果は，この砂浜の波浪環境が相対的に穏やかであるということを意味している。これは，検見川の浜において，内側に湾曲して設置された突堤が，沖合からの波浪をある程度，防いでいるためと考えられる（Fig. 1）。この

Table 4. Results of LR tests examining the effects of month and beach on the total numbers of fish species and individuals using a GLM.

	df	LRx^2	p	HBT
Number of species				
Month	3	37.6	<0.001	May=Jul>Sep=Nov
Beach	2	3.5	0.171	
Month×Beach	6	8.5	0.206	
Number of individuals				
Month	3	93.5	<0.001	
Beach	2	4.4	0.110	
Month×Beach	6	47.1	<0.001	
Month in IN	3	8.5	<0.05	—
Month in KM	3	81.1	<0.001	May=Jul>Sep=Nov
Month in MK	3	84.9	<0.001	May>Sep=Jul>Nov
Beach in Sep.	2	3.8	0.148	
Beach in Nov.	2	3.6	0.167	
Beach in May	2	20.1	<0.001	MK>IN
Beach in July	2	92.6	<0.001	KM>IN=MK

For abbreviations, see Table 1.
HBT was conducted when the GLM and LR test results indicated significant effects.

ような波浪環境では，海底の撹乱は少なく，デトリタスが沈殿しやすい状態となることが予測される。検見川の浜において，強熱減量が高かったのは，このためであると考えられる。

4.2　生物的環境

　調査した生物的環境項目のうち，月間の違いが3つ砂浜で同様にみられたのは，浮遊性無脊椎動物と表在性無脊椎動物の総個体数，およびアミ類（表在性無脊椎動物）の個体数であった。浮遊性無脊椎動物の総個体数は9月で，また表在性無脊椎動物の総個体数とアミ類の個体数は5月で最も多かった。浮遊性無脊椎動物において優占したカイアシ類（カラヌス類やキクロプス類）は，南日本の沿岸浅海域では夏に多いことが知られている（広田，1998; INOUE et al., 2008）。また，アミ類は初夏を中心に多いことが報告されている（広田，1998; INOUE et al., 2008）。したがって，本研究においても同様の結果が得られた。

　一方，調査期間を通した砂浜間での違いは，埋在性無脊椎動物の総個体数にみられ，検見川の浜で多い傾向にあった。これは，4.1節で述べたよ

うに，検見川の浜では他の砂浜よりも波浪が穏やかで，デトリタスが沈殿しやすかったためと考えられる。デトリタスは多毛類を含む多くの埋在性無脊椎動物の餌となることが知られている（堀越・菊池，1976）。

4.3　魚類群集の構造
4.3.1　採集された魚類

　調査期間を通して3つの砂浜で採集された魚類は，主に稚魚であった。自然の砂浜では成魚と比べ，稚魚が多く生息することが，日本を含めた世界各地から報告されており（e.g., LASIAK, 1986; 須田，2002; BENAZZA et al., 2015; 井上，2017; MCLACHLAN and DEFEO, 2018; OLDS et al., 2018），本調査地においても同様の結果となった。特に，優占種のスズキ，イシガレイ，コノシロ，トウゴロウイワシ，アユの5種については，すべての個体が稚魚であった。これらの優占種は特定の月や砂浜において多く採集され，スズキは5月の幕張の浜に，イシガレイとアユは5月の検見川の浜に，コノシロは7月の検見川の浜に，トウゴロウイワシは9月のいなげの浜に多かった。東京湾の浅所

Bray-Curtis similarity index
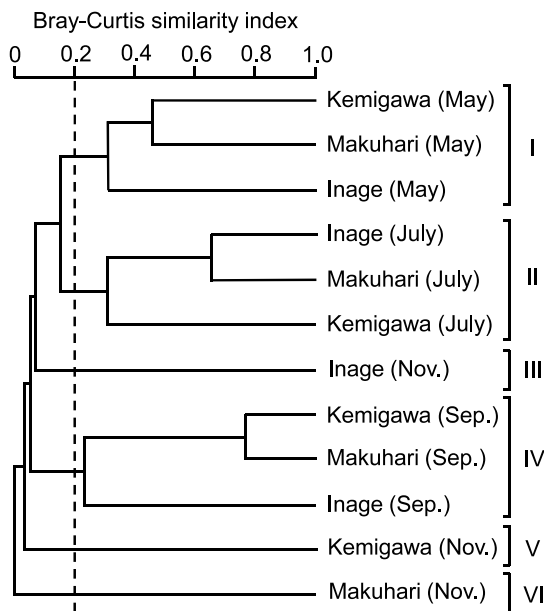
Fig. 5 Dendrogram of a cluster analysis showing similarities of fish assemblages, based on number of individuals of each fish species on each artificial sandy beach (Inage, Kemigawa and Makuhari) in September and November 2017, and May and July 2018. Assemblages divided into six groups (I–VI) at a Bray-Curtis similarity index level of 0.2.

では，本研究結果と同様に，これら5種の稚魚は上記した特定の月や季節に出現することが知られている（加納・横尾，2011）。以下では，それぞれの種の個体数がなぜ砂浜間で異なったのか，その理由について考察する。

　スズキの稚魚は5月の幕張の浜で多かった。5月に幕張の浜と他の砂浜の間で違いがみられた物理・生物的環境項目をみると，それらは表在性無脊椎動物の総個体数とアミ類の個体数であった。両項目は統計的には有意でないものの，幕張の浜で多い傾向にあった。本種の稚魚は主にアミ類を食べて成長するため（Table 3），アミ類をはじめとする表在性無脊椎動物の多い5月の幕張の浜は，稚魚の有効な餌場となっていた可能性がある。このために，スズキの稚魚は5月の幕張の浜で多

かったのかもしれない。

　イシガレイの稚魚は5月において検見川の浜で多く採集された。5月の物理・生物的環境のうち，検見川の浜と他の砂浜との間で違いがみられた項目は，塩分，波高，波浪周期，強熱減量，浮遊性無脊椎動物と埋在性無脊椎動物の総個体数，多毛類の個体数であった。ただし，塩分は砂浜間の差がわずかであったため（Fig. 2），魚類の分布に大きな影響は与えないものと考えられる。また，イシガレイの稚魚は多毛類食であるため（Table 3），浮遊性無脊椎動物の総個体数も本種の分布に大きな影響は及ぼさないものと思われる。一方，波高は検見川の浜で低く，波浪周期はその逆の傾向を示し，検見川の浜で長かった。これは検見川の浜の波浪環境が相対的に穏やかであることを示している。本種のような底生魚は厳しい波浪にある程度は耐えられることが知られているが（TATEMATSU *et al.*, 2014），魚類全般についてみると，波浪の穏やかな環境では遊泳力に乏しい稚魚や小型魚が多く出現する（NAKANE *et al.*, 2013; TATEMATSU *et al.*, 2014; 荒山・河野，2015; OLDS *et al.*, 2018）。本研究で採集されたイシガレイ稚魚は，まだ体長の小さな個体であったため（Fig. 7），波浪の穏やかな環境を好んで生息する可能性がある。また，検見川の浜では，本種の稚魚の餌となっている多毛類や埋在性無脊椎動物の個体数が多かった。以上のことから，5月の検見川の浜は他の砂浜よりも波浪が穏やかで，多毛類を含む埋在性無脊椎動物が多い環境であったため，イシガレイ稚魚は検見川の浜に多く出現した可能性がある。

　コノシロは7月において検見川の浜で多く採集されたが，物理・生物的環境の中で検見川の浜と他の砂浜との間で異なった項目は，波高，強熱減量，埋在性無脊椎動物の総個体数，アミ類と多毛類の個体数であった。波高は検見川の浜で低く，それとは逆に強熱減量は検見川の浜で高かった。これは，上述したように，検見川の浜は他の砂浜よりも波浪が穏やかで，デトリタスが多いためである。本種の稚魚はデトリタス食であり（Table 3），また検見川の浜で採集された多くの
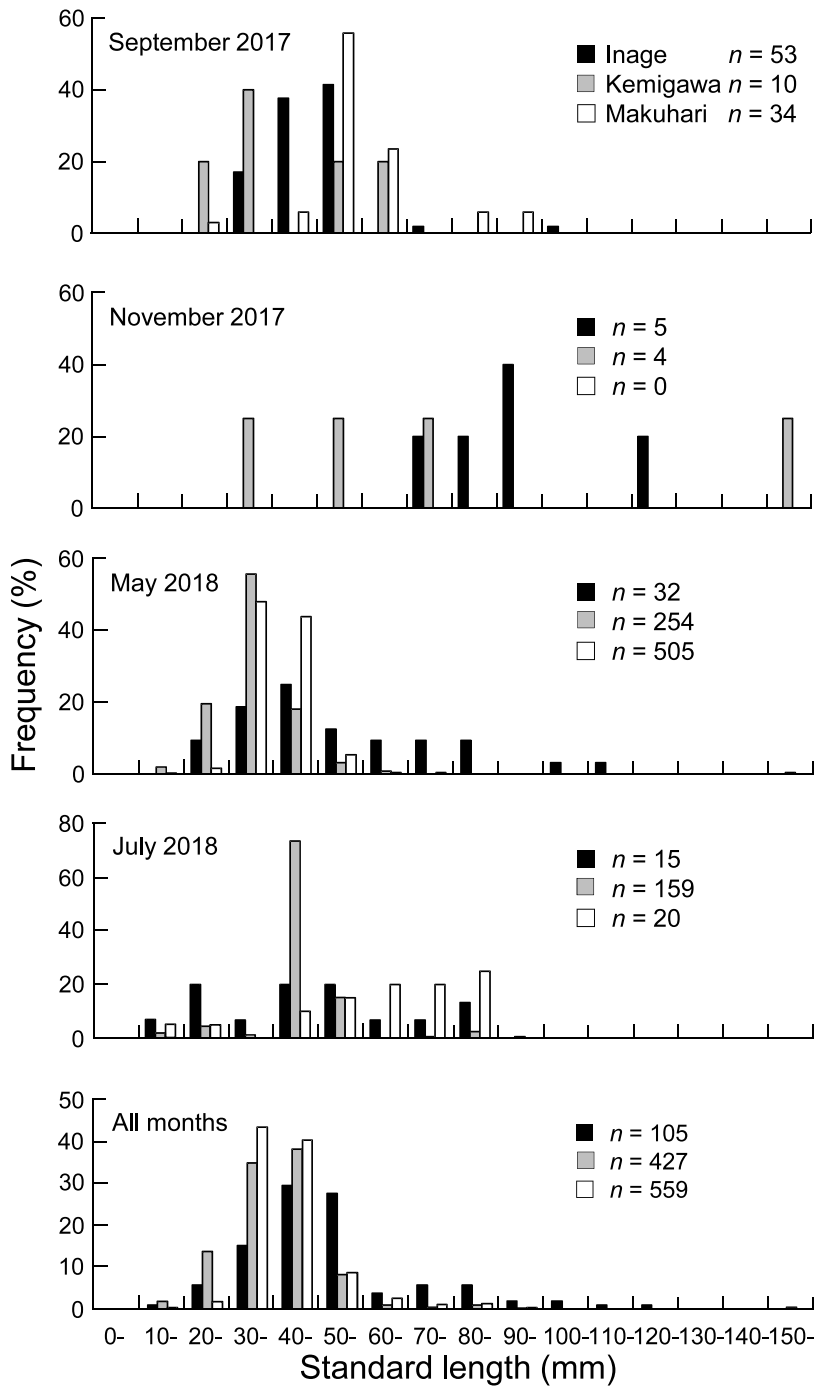
Fig. 6 Frequency distributions of standard lengths of all fishes collected on Inage, Kemigawa and Makuhari beaches in each month (September and November 2017 and May and July 2018).

Table 5. Results of LR tests examining the effects of month and beach on standard lengths of all fishes collected during the study period and of *Lateolabrax japonicus* and *Platichthys bicoloratus* collected in May using a GLM.

	df	LRx^2	p	HBT
All fishes				
Month	3	330.8	<0.001	
Beach	2	96.9	<0.001	
Month×Beach	5	95.7	<0.001	
Month in IN	3	31.6	<0.001	Nov>Sep=May=Jul
Month in KM	3	128.5	<0.001	Nov>Sep, Nov>Jul>May
Month in MK	2	354.9	<0.001	Sep=Jul>May
Beach in Sep.	2	22.7	<0.001	MK>IN=KM
Beach in Nov.	1	0.4	0.521	
Beach in May	2	149.2	<0.001	IN>MK>KM
Beach in July	2	31.2	<0.001	MK>IN=KM
L. japonicus in May				
Beach	1	9.0	<0.01	MK>KM
P. bicoloratus in May				
Beach	2	56.8	<0.001	IN>MK>KM

For abbreviations, see Table 1.
HBT was conducted when the GLM and LR test results indicated significant effects.

稚魚は体長 50 mm 以下の小型魚であった。したがって，コノシロが 7 月の検見川の浜で多かった理由としては，餌のデトリタスが他の砂浜よりも多く存在したことや，波浪が穏やかであったことが考えられる。

トウゴロウイワシは 9 月のいなげの浜で多かった。9 月にいなげの浜と他の砂浜との間で違いがみられた物理・生物的環境項目は，水温，濁度，浮遊性無脊椎動物の総個体数であった。ただし，水温と濁度については，砂浜間での差がわずかであったため（Fig. 2），魚類の分布にはほとんど影響を与えないものと考える。一方，浮遊性無脊椎動物の総個体数はいなげの浜で顕著に多かった。本種の稚魚は，カラヌス類やキクロプス類などを食べる浮遊性無脊椎動物食魚である（Table 3）。したがって，浮遊性無脊椎動物が多かった 9 月のいなげの浜は，トウゴロウイワシの稚魚にとって重要な餌場となっていた可能性があり，そのために個体数が多かったのかもしれない。

アユは 5 月において検見川の浜でのみ採集された。本種の稚魚は浮遊性無脊椎動物食であるが（Table 3），5 月における浮遊性無脊椎動物の総個体数はいなげの浜で多く，検見川の浜では少ない傾向を示した。したがって，本種が検見川の浜でのみ採集されたのは，餌量とは関係なく，別の理由によるものと考えられる。Table 3 をみると，アユと同じ浮遊性無脊椎動物食であるボラ *Mugil cephalus cephalus* の稚魚は，5 月の検見川の浜において多く採集されていることがわかる。ボラの稚魚は表層遊泳魚であるため，波浪環境の厳しい場所を避け，穏やかな場所を好むことが知られている（瀧ヶ﨑・佐野，2013; TATEMATSU *et al.*, 2014; 青木ほか，2016）。本研究において，検見川の浜は他の 2 つの浜よりも波浪が穏やかであり，ボラの稚魚が検見川の浜で多かったのは，このためであると考えられる。アユの稚魚も表層遊泳魚であるため，ボラの稚魚と同様の理由で，検見川の浜に多く分布していたのかもしれない。
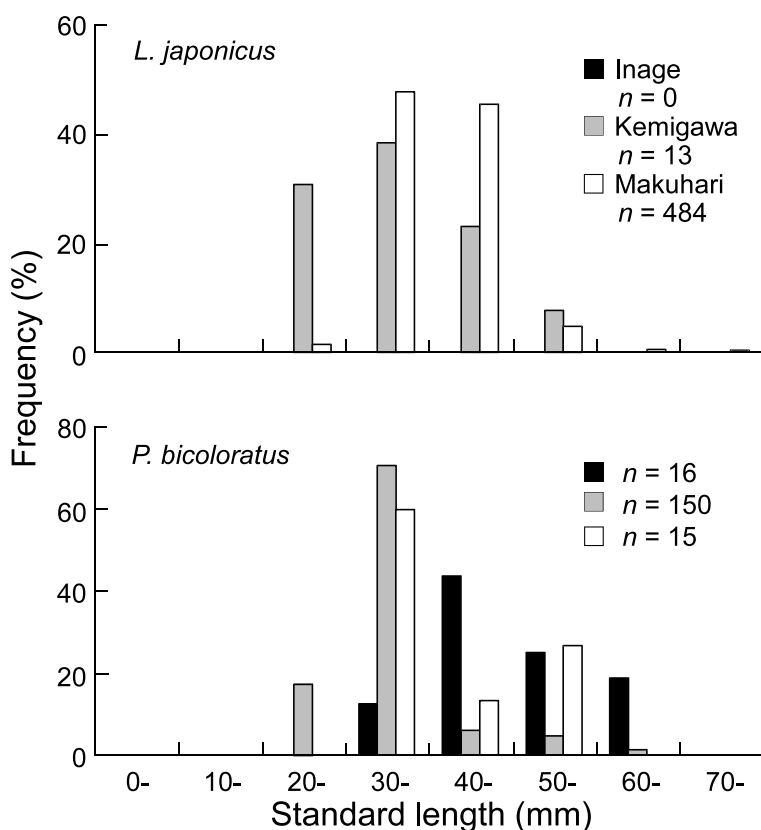
Fig. 7 Frequency distributions of standard lengths of the two most domi-
nant fish species, *Lateolabrax japonicus* and *Platichthys bicoloratus,* col-
lected on each artificial sandy beach in May 2018.

4.3.2 種数と総個体数

　一曳網（300 m²）あたりの魚類の種数は月間で
有意な差がみられ，5月，7月に多く，9月，11月
で少なかった。また，一曳網あたりの総個体数は，
いなげの浜では9月が他の月よりもやや多い傾向
にあったものの，検見川や幕張の浜では5月に多
かった。したがって，本調査地における魚類の種
数と総個体数は概ね春に多く，秋に少ないという
傾向が認められた。このような季節変化は自然砂
浜からも報告されている（Suda *et al.,* 2002;
Selleslagh and Amara, 2007; Inoue *et al.,* 2008; 岩
本ほか，2009）。

　次に，各月の砂浜間による違いをみると，種数

については有意な差はみられず，どの砂浜も同じ
ような種数を示す傾向にあった。一方，総個体数
では5月と7月にそれぞれ差が認められた。しか
し，それらの差は月ごとに異なったパターンを示
し，5月では幕張，検見川，いなげの浜の順に多
く，7月では検見川の浜がいなげや幕張の浜より
も多かった。したがって，調査期間を通してみた
場合，総個体数においても種数と同様に，砂浜間
での違いは明瞭ではなかったといえる。

　既往研究では，砂浜における魚類の種数と総個
体数は波浪の穏やかな場所で多くなることが報告
されている（e.g., Romer, 1990; Clark, 1997; Inui *et
al.,* 2010; Nakane *et al.,* 2013; Tatematsu *et al.,*
2014）。本調査地においては調査期間を通して，

波浪は検見川の浜で他の砂浜よりも穏やかであった。また，強熱減量や埋在性無脊椎動物の総個体数も検見川の浜で高い値を示した。それにもかかわらず，魚類の種数と総個体数は砂浜間で明瞭に異なってはいなかった。したがって，本調査地でみられた波浪などの環境の違いは，優占種の分布に影響を与えた可能性はあるものの（4.3.1 項参照），魚類の種数や総個体数にはあまり影響を及ぼさなかったと考えられる。以上のことから，本調査地における魚類の種数と総個体数は砂浜間よりも季節間で異なることが明らかとなった。

4.3.3 種組成

クラスター分析の結果，種組成は主に月によって分かれた。これは，優占種を含む多くの魚種が，特定の月でのみ採集されたためであると考えられる（Table 3）。また，このような魚種では，ほとんどの個体が稚魚であった。稚魚の出現する季節や月は，魚種によってそれぞれ異なることが知られており（加納・横尾，2011），本調査地においても同様な結果が得られた。これらの結果は，多くの魚類にとって，本調査地の砂浜は稚魚期の一時期を過ごす場所となっていることを示唆する。

また，各月における砂浜間の類似パターンは月ごとに異なっており，調査期間を通した一定のパターンは認められなかった。したがって，種組成は砂浜間で明らかに異なるとはいえなかった。以上のことから，本調査地における魚類の種組成は，種数と総個体数と同様に，砂浜間よりも季節間で異なることが明らかとなった。

4.3.4 体長

採集された魚類全個体の体長は，すべての砂浜において月間で有意な差がみられ，いなげや検見川の浜においては 11 月が他の月よりも大きい傾向にあった。また，幕張の浜では 9 月と 7 月が 5 月よりも大きかった（11 月は魚類が採集されなかった）。したがって，本調査地においては概ね 5 月から 11 月にかけて季節がすすむほど，体長の大きい魚類が採集されたといえる。このような傾向は，日本の自然砂浜においても報告されている

（NANAMI and ENDO, 2007; 須田ほか，2014）。

全個体の体長について各月の砂浜間で比較したところ，11 月を除いた各月で有意差がみられ，検見川の浜で小さい傾向が認められた。また，優占種のスズキとイシガレイにおける 5 月の体長も検見川の浜で小さかった。検見川の浜はいなげや幕張の浜よりも波浪が穏やかであることから，4.3.1 項で述べたアユやボラと同様に，遊泳力に乏しい小型の稚魚がそのような環境を好み，多く出現したと考えられる。

5. 結論

本研究により，千葉市美浜区の埋立地に造成された人工砂浜（いなげの浜，検見川の浜，幕張の浜）では，自然の砂浜と同様に，稚魚を中心とした魚類群集が形成されることが明らかとなった。特に，個体数の多かった魚種では，稚魚期における餌場や波浪からの避難場として，これらの砂浜を利用している可能性が示唆された。また，種数や総個体数，種組成，体長においては，自然の砂浜でみられるような季節変化が認められた。以上のことから，本調査地の人工砂浜は自然の砂浜に近い機能をもち，稚魚にとっての重要な生息場の 1 つとなっていることが示唆された。砂浜を含む浅海の沿岸域は，港湾建設や埋め立てなどによる人工改変を受けやすい場所であり，特に東京湾の内湾では自然の砂浜や干潟はほとんど残っていない（荒山ほか，2002; 青木ほか，2016）。そのような中にあって，本調査地のような砂浜は魚類の重要な生息場として，今後，適切に管理される必要があると思われる。

本研究では，3 つの人工砂浜間における魚類群集構造の違いについても調べた。検見川の浜はいなげの浜や幕張の浜と異なり，内側に湾曲した突堤が砂浜の両端にあるため，保護的な環境となっていた。このため，波高，強熱減量，埋在性無脊椎動物の総個体数に砂浜間で違いが認められた。これらの物理・生物的環境の違いは魚類の種数，総個体数，種組成には影響を与えなかったが，体長においてはその影響が示唆され，検見川の浜では体長の小さな個体が出現する傾向にあった。こ

れは，遊泳力に乏しい小型の稚魚が，波浪の影響を避けるために，穏やかな検見川の浜に分布したためであると考えられる。また，本調査地において多く採集されたイシガレイ，コノシロ，アユの稚魚も，検見川の浜を餌場とともに，波浪からの避難場として利用していた可能性が示唆された。このように，突堤の形状は砂浜における物理・生物的環境に影響を与え，多少なりとも魚類群集の構造を変える可能性がある。このため，人工砂浜の造成の際に突堤を建設する場合は，その形状についても考慮する必要があると思われる。

謝　辞

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Occurrence patterns and ontogenetic development based on the swimming- and feeding-related characters in larval and juvenile Japanese whiting (*Sillago japonica*) in the innermost Tokyo Bay, central Japan

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Abstract: Occurrence patterns of the larval and juvenile Japanese whiting, *Sillago japonica*, were investigated in Tokyo Bay by monthly samplings using the following two types of gear: a small seine net towed at three tidal-flat stations around the river mouth of Tama-gawa River from May 2006 to September 2009; and a ring net towed at a station in the offshore water of the Tama-gawa River mouth from January 2006 to May 2008. Their functional development was also observed mainly by osteological characters on the basis of 111 cleared and stained specimens of 2.0–21.1 mm in body length (BL). Specimens collected from the offshore water were 30 in number with 4.6 ± 1.6 (mean ± SD) mm BL, ranging from 2.0 to 8.5 mm BL, and those from the tidal flats were 232 with 15.7 ± 5.6 mm BL from 6.1 to 49.3 mm BL. Based on the functional development of swimming- and feeding-related characters, the larvae and juveniles were divided into five and four developmental phases, respectively. Improvements of swimming and feeding functions observed at about 3 mm BL were considered to assist the early larvae in migrating shoreward, and the specimens of 6.0–8.9 mm size classes occurred in both the offshore and tidal flat stations. Thereafter on tidal flats, the number of individuals increased and reached a peak at about 15 mm BL, when the juveniles acquired functional swimming and feeding abilities. The juveniles > 15 mm BL decreased in number, and then those ca. 30 mm BL had scarcely appeared on the tidal flats. The Japanese whiting juveniles > ca. 30 mm BL in the innermost Tokyo Bay are most likely to move into deeper waters.

Keywords : *Japanese whiting, early life history, habitat shift, functional development*

1. Introduction

The Japanese whiting, *Sillago japonica*, distrib-

uted in the coasts of Japan from the southern part of Hokkaido to Kyushu, Korea, China and Taiwan (Hayashi and Hagiwara, 2013), is known as an important commercial fish (Sano and Mochizuki, 1984). In Tokyo Bay, which is located in the southeast coast of central Japan and the inner bay of which is surrounded by the Tokyo metropolitan area, the Japanese whiting is also a target fish for fisheries and angling. Therefore,

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many studies have been conducted for knowing the biological aspects of the species as follows: the spawning patterns (SULISTIONO *et al.*, 1999a), age and growth (SULISTIONO *et al.*, 1999c), feeding habits (SULISTIONO *et al.*, 1999b; ARAYAMA and KOHNO, 2004), and concentrations of radioactive cesium (YANAGITA *et al.*, 2016; TEISHIMA *et al.*, 2017). Furthermore, their occurrence patterns have been studied in offshore-surface waters by ring nets (e.g. KANOU *et al.*, 2002a; NAGAIWA *et al.*, 2005), tidal flats/surf zones by seine nets (e.g. NASU *et al.*, 1996; KANOU *et al.*, 2000; ARAYAMA *et al.*, 2002; AOKI *et al.*, 2016; UMEDA and KOHNO, 2017), and offshore-bottom waters by beam trawl nets (YONEYAMA *et al.*, 2009; BUREAU OF ENVIRONMENT, TOKYO METROPOLITAN GOVERNMENT, 2018).

McKAY (1992) compiled the information about habitat, biology and fisheries of the species. However, no studies are available on the development of swimming- and feeding-related characters, the functional development, nor the ontogenetic intervals; although OOZEKI *et al.* (1992) divided laboratory-reared larvae and early juveniles into 10 stages and 3 phases on the basis of morphological and histological characters, no detailed descriptions were given and their phases corresponded to yolk-sac, from pre- to postflexion and transformation larvae of KENDALL *et al.* (1984).

This study aims to establish the ontogenetic intervals during the early life history of the Japanese whiting based on the development of swimming- and feeding-related characters. The occurrence patterns of larvae/juveniles are also investigated in offshore waters and on tidal flats in the inner Tokyo Bay, and the relationships between the ontogenetic intervals and occurrence patterns are clarified to elucidate how each area of the inner Tokyo Bay provide habitats for the species.

2. Material and methods

Specimens used in this study were sampled from four sampling sites in the inner Tokyo Bay (Fig. 1). Two types of sampling gear were used as follows: a 0.8 mm mesh size small seine net (cf., KANOU *et al.*, 2002b) was monthly or bimonthly towed for about 100 m^2 at about 1m depth tidal flat during day time from May 2006 to September 2009 in three stations around the river mouth of Tama-gawa River, the northwestern innermost Tokyo Bay; and a 1.3 m diameter ring net with 0.5 mm mesh size was towed for 15 minutes by one to two knots through surface waters during day time from January 2006 to May 2008 (not sampled in March and July 2006, and January, March, July and September 2007) in one station off the mouth of Tama-gawa River by a 19 ton T/S *Hiyodori* of Tokyo University of Marine Science and Technology. Water temperature and salinities were measured after the samplings from January (offshore) or May (tidal flats) 2006 to May 2008, and the sediment was collected from the bottom of tidal flats for the measurements of particle-size distribution and mud-content percentage (cf., KOHNO *et al.*, 2014) from March 2008 to September 2009.

Collected specimens were fixed in 5% seawater formalin and later preserved in 70% ethanol. Species identification follows OKIYAMA (2014). The body length (BL: *sense* LEIS and TRNSKI, 1989) of each specimen was measured to the nearest 0.1 mm using a micrometer attached to a binocular dissecting microscope or a digital caliper.

Out of the specimens collected, 111 individuals (2.0–21.1 mm BL) were randomly selected for the morphological study to establish the ontogenetic intervals. These specimens were cleared and stained by the method of POTTHOFF (1984), and the following characters were observed: as the swimming-related characters, fin supports
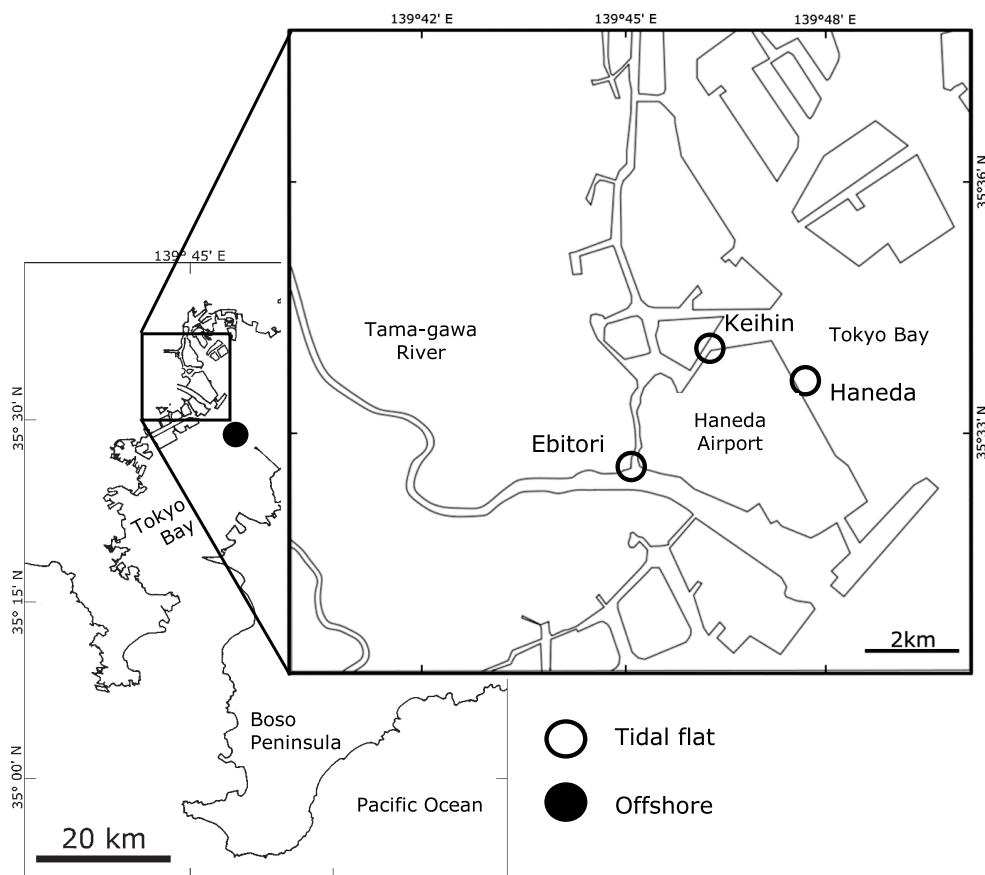
Fig. 1 Map showing the locations of one offshore and three tidal-flat sampling stations in the inner Tokyo Bay, central Japan.

and rays, the angle of notochord flexion (measured until the urostyle appeared and the notochord tip disappeared), vertebral centra, hemal and neural arches and spines, and the greatest body depth and its position measured from the snout tip to the vertical line at the greatest body depth; and as feeding-related characters, the structure of upper jaw (maxilla and premaxilla), the structure of lower jaw (Meckel's cartilage, dentary, angular and retroarticular), mouth width, ratio of premaxilla to gape, numbers of jaw teeth, pharyngeal teeth, and prevomer teeth, suspensorium, opercular bones, hyoid arch, and number of branchiostegal rays. The histogram

method of developmental events by 1 mm BL fish size intervals employed by SAKAI (1990) and the key character method of KOHNO and SOTA (1998) and KOHNO *et al.* (2000) were both applied to determine the ontogenetic intervals (cf., SHINAGAWA *et al.*, 2002). In this study, the description was based on the body length in the state of ethanol preservation and on the smallest specimen when the developmental phenomena and events were first observed.

3. Results

3.1 Physical conditions of water and sediment

The water temperature in the offshore and
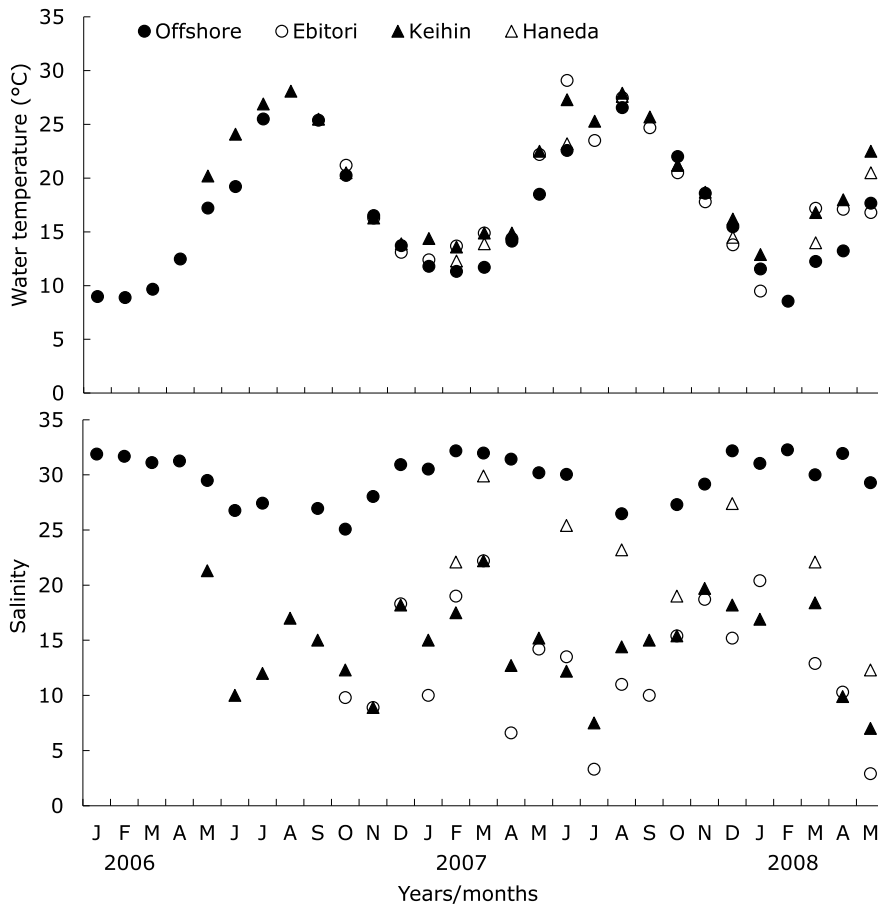
Fig. 2　Water temperature and salinities of the offshore and three tidal-flat sampling
　　　　stations in the inner Tokyo Bay.

tidal-flat stations showed such the same tenden-
cy as increasing during the summer season and
decreasing during the winter season, and no
remarkable differences were detected between
the stations（Fig. 2）. The highest temperature,
29.1 ℃, was recorded at the river tidal flat sta-
tion, Ebitori, in June 2007 and the lowest, 8.5 ℃,
at the offshore station in February 2008.

　The salinity was the highest in the offshore
station, ranging from 25.1 to 32.3 with the mean
± SD = 29.9 ± 2.1, followed by the forehead
tidal-flat station, Haneda, ranging from 12.3 to
29.9 with 22.8 ± 4.1（Fig. 2）. In the river-mouth

and river tidal-flat stations, Keihin and Ebitori,
the salinities were relatively low and varied from
3.0 to 22.2 with 14.4 ± 3.9 and from 0.1 to 22.2
with 11.4 ± 5.2, respectively.

　Regarding the bottom sediment, the median
particle size was the largest and the mud-
content percentage was the lowest in Haneda,
varying from 326.8 to 1,358.3 µm（mean ± SD =
621.4 ± 307.2 µm）and from 0.6 to 8.0 %（1.2 ±
0.4 %）, respectively（Fig. 3）. No remarkable dif-
ferences were observed in the bottom sediment
between Keihin and Ebitori; the median particle
size and mud-content percentages fluctuated
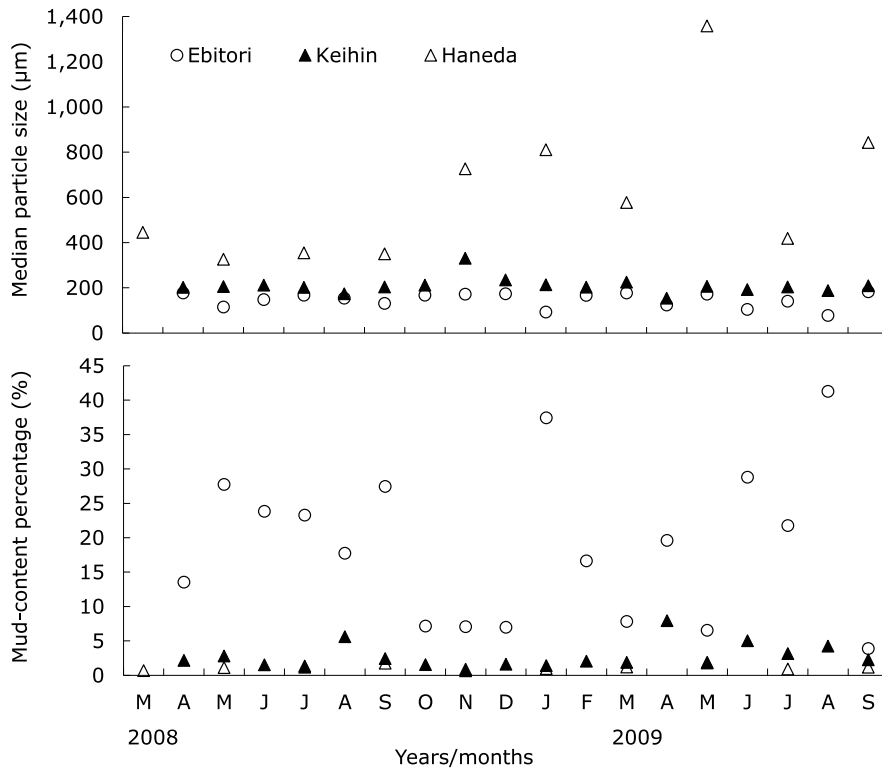
Fig. 3 Median particle size and mud-content percentage of the bottom sediment at three tidal-flat sampling stations around the Tama-gawa River mouth in the inner Tokyo Bay.

from 154.3 to 331.1 μm (209.7 ± 34.2 μm) and from 0.7 to 8.0 % (2.8 ± 1.8 %) in the former and from 78.1 to 182.7 μm (146.9 ± 31.2 μm) and from 3.9 to 41.3 % (18.8 ± 10.8 %) in the latter.

3.2 Occurrence patterns

The total number of Japanese whiting collected from the offshore station was 30 with the size of 4.6 ± 1.6 mm BL (mean ± SD), ranging from 2.0 to 8.5 mm BL, with a mode of 3.0–3.9 mm BL (Fig. 4). The months of occurrence were limited to August (3.4 ± 1.0 mm BL, $n = 8$), September (5.9 ± 2.0 mm BL, 7) and October (4.7 ± 1.3 mm BL, 15) (Fig. 5). In the three tidal-flat stations, no specimens were collected from the river tidal flat station, Ebitori. The total number of specimens collected from the other two tidal-flat stations, Keihin and Haneda, was 232 with the size of 15.7 ± 5.6 mm BL, ranging from 6.1 to 49.3 mm BL and a mode of 14.0–14.9 mm BL (Fig. 4). The BL of specimens collected from the offshore and tidal-flat stations were overlapped in 6.0–8.9 mm size classes (Fig. 4).

The specimens collected from the river mouth tidal flat station, Keihin, numbered 95, ranging from 6.1 to 49.3 mm BL (17.2 ± 6.3 mm BL) with a mode of 14.0–14.9 mm BL (Fig. 6). The months of occurrence were limited to the period from July to September, and the number and size of specimens by the months were $n = 4$ and 14.8 ± 3.9 mm BL ranging from 10.0 to 18.5 mm BL in July, 57 and 19.3 ± 7.2 mm BL from 6.1 to 49.3
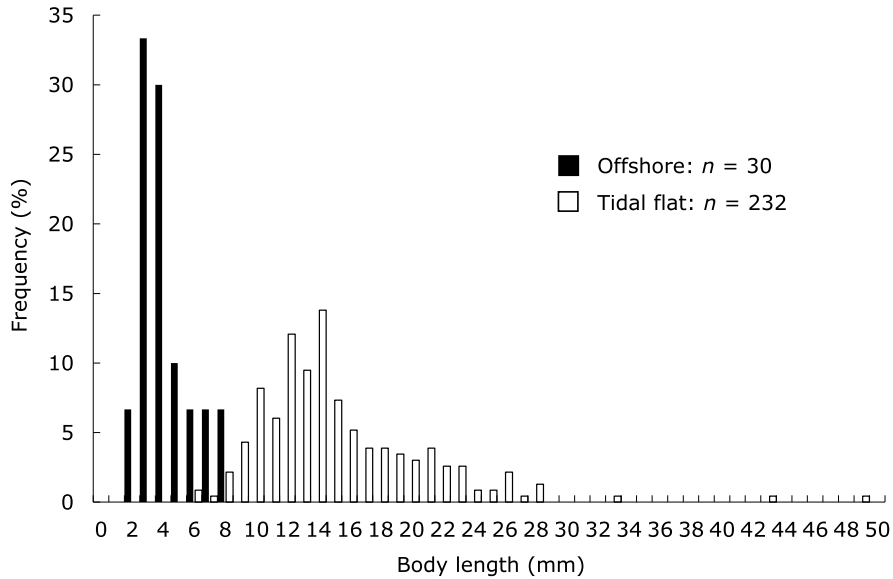
Fig. 4 Size composition of the Japanese whiting, *Sillago japonica*, collected from the offshore and three tidal-flat sampling stations in the inner Tokyo Bay.

mm BL in August, and 34 and 14.0 ± 1.8 mm BL from 10.3 to 17.5 mm BL in September（Fig. 7）.

In the forehead tidal flat station, Haneda, the number of specimens collected was 137 ranging from 6.4 to 43.2 mm BL（14.7 ± 4.7 mm BL）with a mode of 14.0–14.9 mm BL（Fig. 6）. These specimens were collected from July to October, and the monthly changes of their individual number and size were as follows （Fig. 7）: $n = 7$ and 12.9 ± 4.8 mm BL（mean ± SD）with a range from 8.9 to 21.3 mm BL in July; 46 and 16.1 ± 4.8 mm BL from 8.8 to 28.0 mm BL in August; 9 and 12.6 ± 4.1 mm BL from 8.7 to 22.2 mm BL in September; and 75 and 14.2 ± 4.7 mm BL from 6.4 to 43.2 mm BL in October.

3.3　Functional development
3.3.1　Swimming-related characters
Flexion of the notochord end: Flexion of the notochord end was first evident at 3.4 mm BL with the angle of 6°, although the largest specimen with a straight notochord end was 4.2 mm BL

（Fig. 8A）. Notochord flexion was complete at about 5 mm BL with the angle of about 40 to 50°.

Caudal fin supports and fin rays: No elements of the caudal skeleton were detected until 2.8 mm BL, when three cartilaginous buds of parhypural and hypurals 1 + 2 and 3 + 4 were observed. The cartilaginous buds of neural and hemal arches and spines of the future preural centrum 4 appeared at 5.3 mm BL and those of the preural centra 2 and 3 and three epurals at 6.2 mm BL. The cartilaginous bud of hypural 5 appeared at 6.5 mm BL, when all the cartilaginous elements were observed; in addition, the hypurals 1 + 2 and 3 + 4 started ossifying. The parhypural, hemal and neural arches and spines of the preural centrum 4, those of the preural centra 2 and 3, and hypual 5 started ossifying at 6.8 mm BL, 7.3 mm BL, 7.6 mm BL, and 7.8 mm BL, respectively. Ossification was perceived in the epurals 1–3 at 11.1 mm BL, and thus all cartilaginous elements started ossifying. The bony urostyle and uroneurals 1 and 2 were first ob-
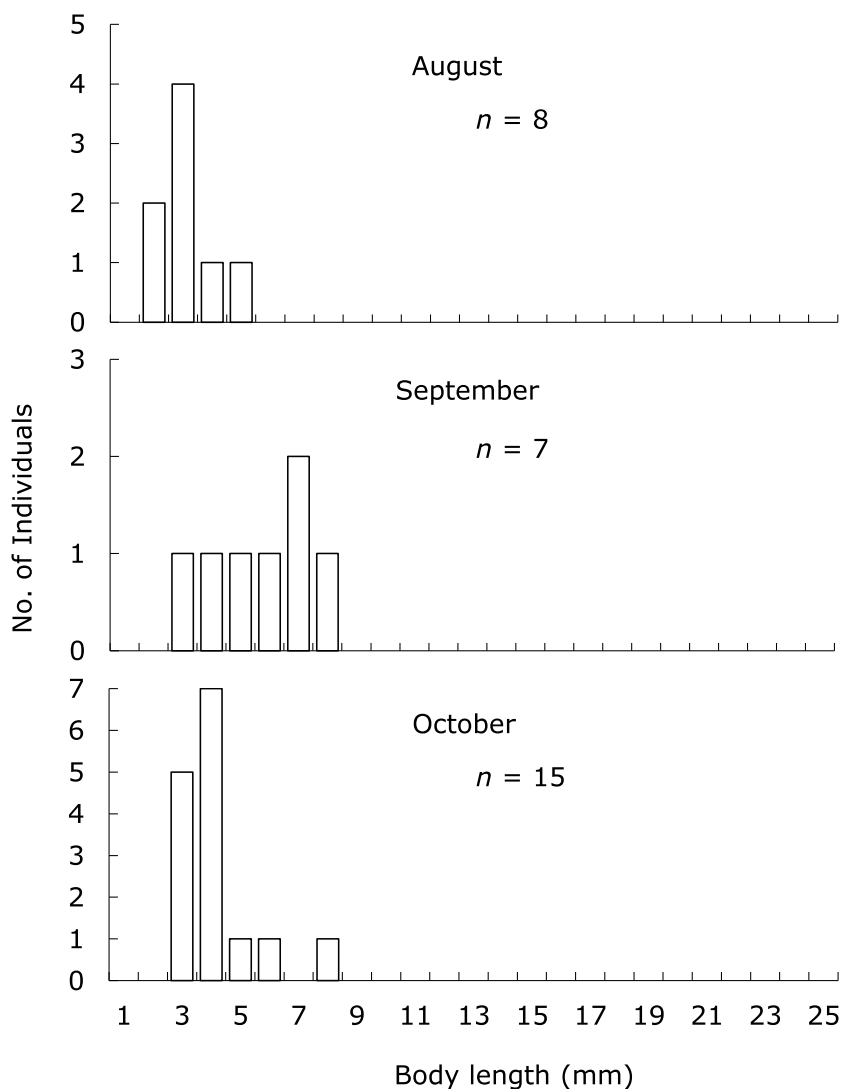
Fig. 5 Monthly changes of the size composition of Japanese whiting, *Sillago japonica*, collected from the offshore sampling station in the inner Tokyo Bay.

served at 5.9 mm BL, 8.3 mm BL and 10.6 mm BL, respectively.

Principal caudal fin rays were first discerned at 2.8 mm BL, when four rays were counted (Fig. 8B). The adult complement of 9 + 8 principal caudal fin rays was attained at 4.9 mm BL.

Dorsal fin supports and fin rays: The smallest specimen with dorsal fin supports was 4.8 mm

BL, in which 23 cartilaginous pterygiophores were observed. All the pterygiophores appeared by 5.9 mm BL. Ossification of five pterygiophores was first observed at 7.9 mm BL, and all elements started ossifying at 13.2 mm BL.

Dorsal fin rays were first discerned at 4.6 mm BL, when 14 soft fin rays were observed (Fig. 8C). The adult complement of 32–35 rays
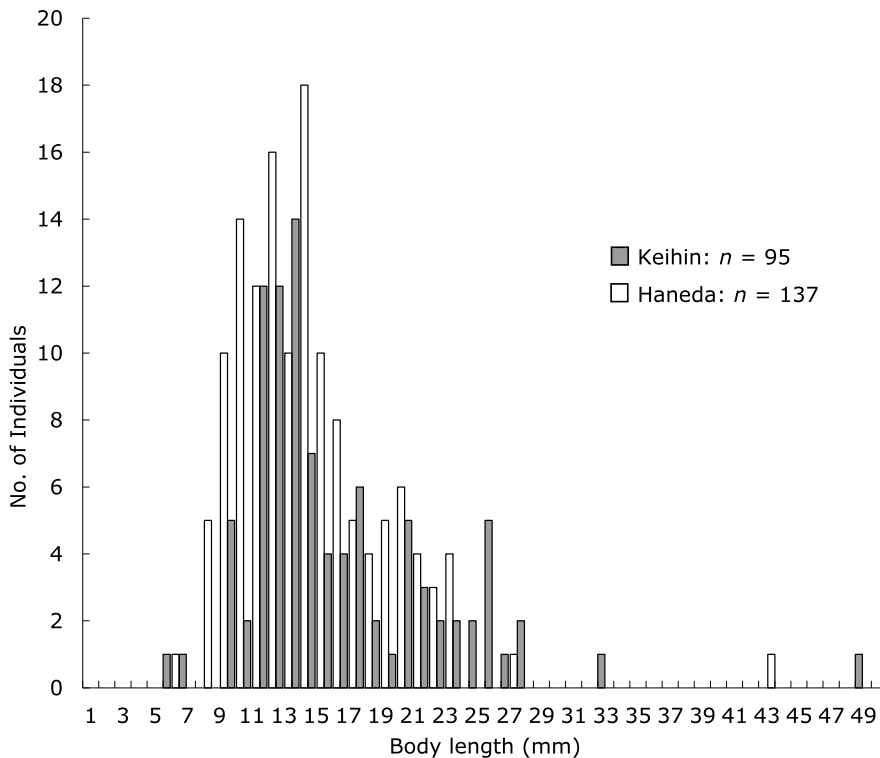
Fig. 6 Size composition of the Japanese whiting, *Sillago japonica*, collected from two tidal-flat sampling stations, the river-mouth tidal flat, Keihin, and the forehead tidal flat, Haneda, in the inner Tokyo Bay.

was attained at 5.9 mm BL.

Anal fin supports and fin rays: Nineteen cartilaginous pterygiophores were first observed at 4.8 mm BL, and all the pterygiophores appeared by 5.9 mm BL. Ossification was first discerned at 7.9 mm BL, and all elements started ossifying at 14.0 mm BL.

Anal fin rays were first discerned at 4.6 mm BL, when 15 soft fin rays were observed (Fig. 8D). The adult complement of 23–26 rays was attained at 5.9 mm BL.

Pectoral fin supports and fin rays: A rod-shaped bony cleithrum, a coraco-scapular cartilage and a cartilaginous plate, which later grew into actinosts, were observed in the smallest specimen examined of 2.0 mm BL. The bladelike

cartilage was divided into four actinosts at 5.9 mm BL. Ossification of the coraco-scapular cartilage and actinosts was first perceived at 7.9 mm BL and 8.5 mm BL, respectively. The bony supracleithrum and posttemporal were observed at 3.6 mm BL and the postcleithrum at 9.4 mm BL.

The pectoral fin rays were first discerned at 5.3 mm BL, when six were noted (Fig. 8E). The adult complement of 15–17 rays was attained at 6.1 mm BL.

Pelvic fin supports and fin rays: The pelvic fin support, the basipterygium, was first observed at 5.9 mm BL, and the ossification started at 9.3 mm BL.

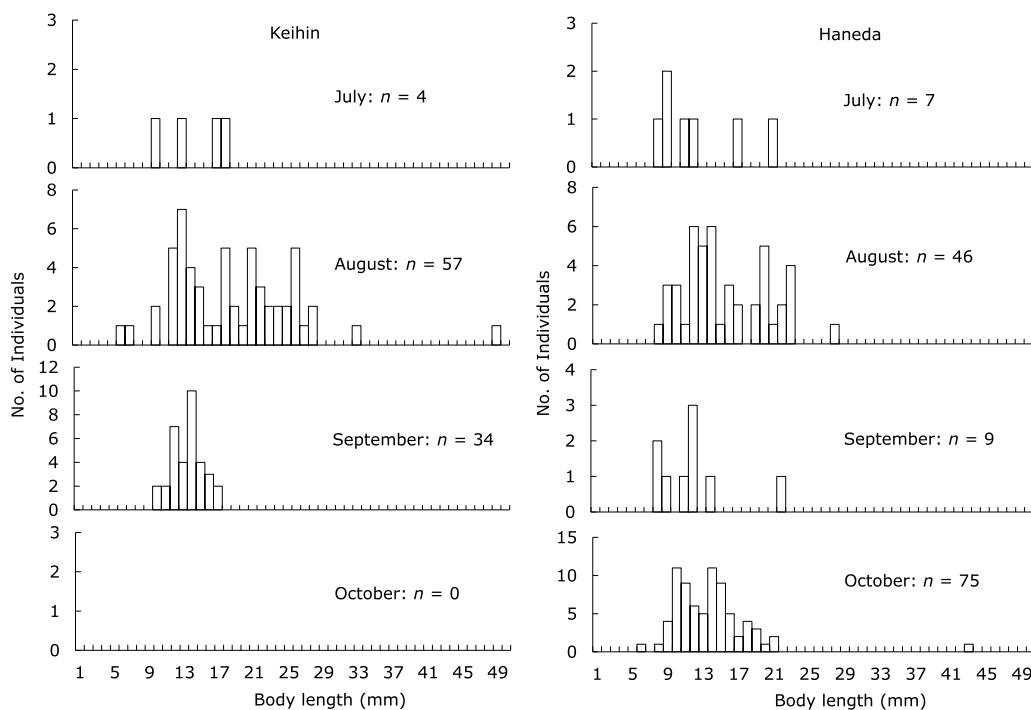The pelvic fin rays were first discerned at 7.2

Fig. 7 Monthly changes of the size composition of Japanese whiting, *Sillago japonica*, collected from two tidal-flat sampling stations, Keihin and Haneda, in the inner Tokyo Bay.

mm BL, when four rays were observed (Fig. 8F). The adult complement of six rays was attained at 9.4 mm BL.

Vertebra: The smallest specimen possessing vertebral elements was 2.8 mm BL, in which 21 centra, 16 cartilaginous neural arches and spines, and seven cartilaginous hemal arches and spines were observed. The adult complement of 35 centra was attained at 5.9 mm BL. Both the hemal and neural arches and spines started ossifying at 6.2 mm BL and became complete in number at 7.7 mm BL. All arches and spines started ossifying at 7.9 mm BL.

Maximum body depth and its position: The ratio of the maximum body depth to BL was 23.5 % in the smallest specimen examined of 2.0 mm BL, although the ratio varied from 11.5–28% until about 8 mm BL (Fig. 8G). The ratios converged

and decreased gradually to 15–20% at about 10 mm BL and became stable thereafter.

The position of maximum body depth varied from 10% at 2.0 mm BL to 35% at 4.0 mm BL (Fig. 8H). The ratios became stable at about 10–25% in specimens of about 9–14 mm BL, but increased to 30–35% thereafter.

3.3.2 Feeding-related characters

Mouth width: The mouth opened in all specimens examined. The mouth width was 0.13 mm in the smallest specimen of 2.0 mm BL and increased rapidly to about 5 mm BL (Fig. 9A). The growth rate became then more or less slow until about 13 mm BL and rapid again, with the largest specimen examined of 21.1 mm BL possessing a 1.88-mm-wide mouth.
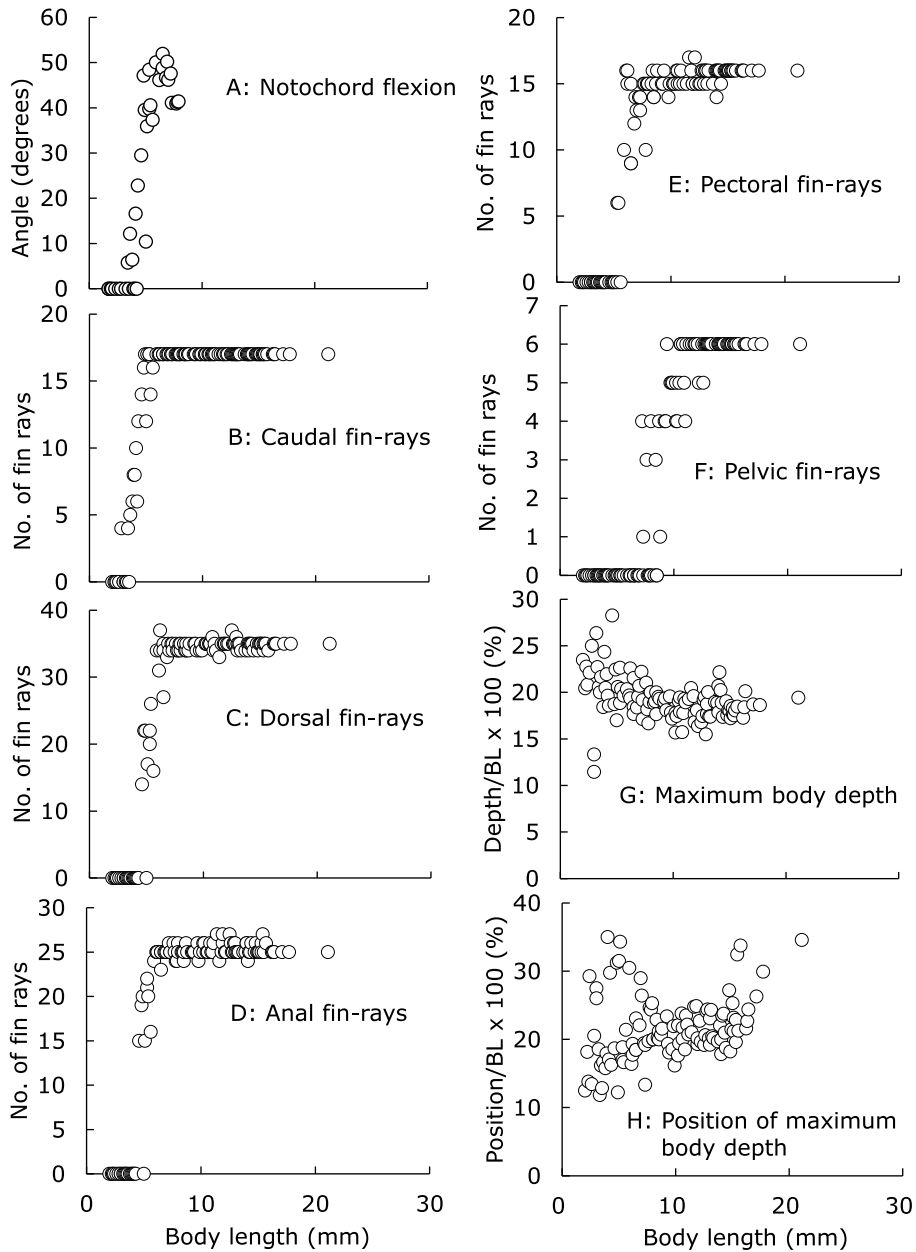
Jaw structure: The smallest specimen of 2.0

Fig. 8 Changes in swimming-related characters with growth in the Japanese whiting, *Sillago japonica.*

mm BL possessed the maxilla and Meckel's carti- lage. Premaxilla and dentary appeared at 2.8 mm BL, the angular at 3.6 mm BL and retroarticular at 4.1 mm BL.

Premaxilla length/gape: The ratio of premaxil- la to gape was 52% at 2.8 mm BL, when the pre- maxilla appeared first (Fig. 9B). The ratio in- creased rapidly to about 85% at about 4 mm BL
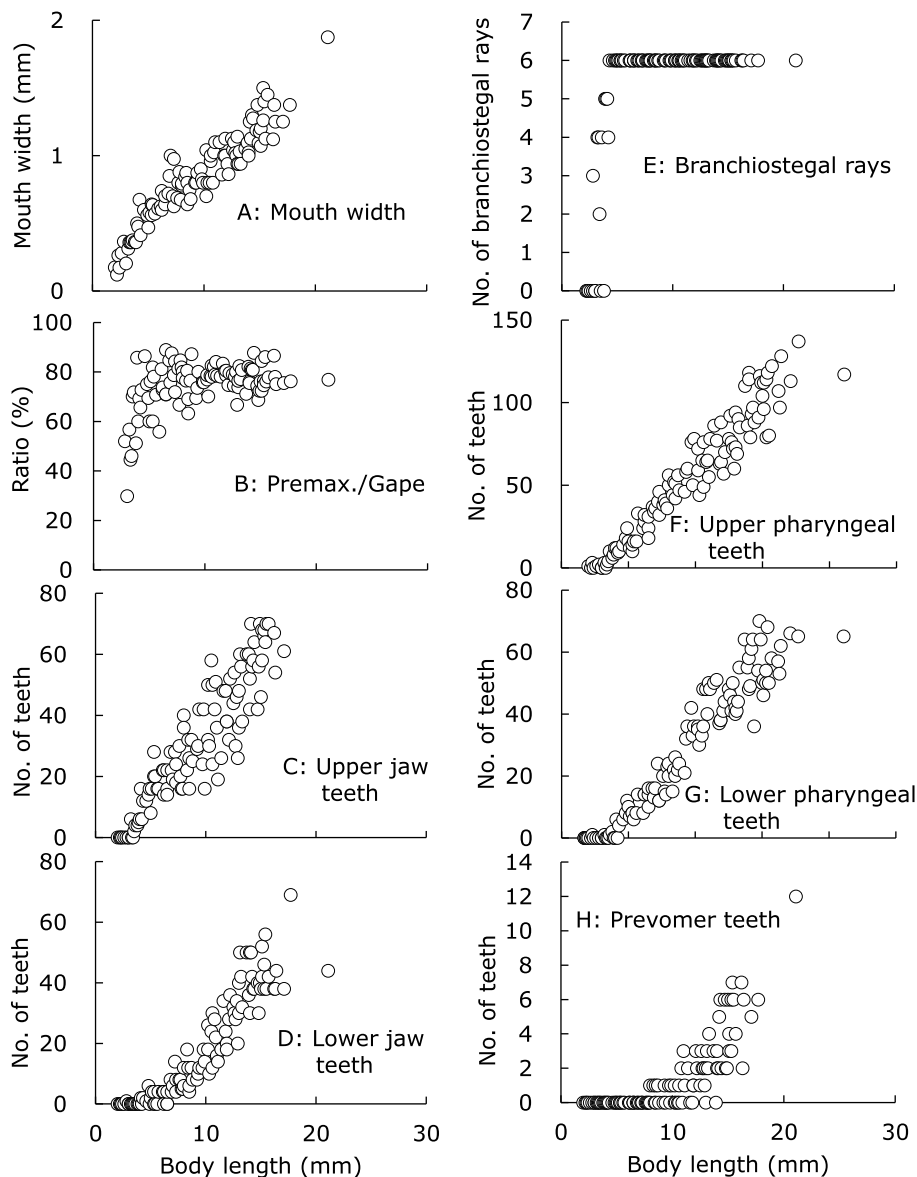
Fig. 9 Changes in feeding-related characters with growth in the Japanese whiting, *Sillago japonica*.

and became stable at 70–85% thereafter.

Jaw teeth: The first upper jaw teeth observed were six in number at 3.2 mm BL（Fig. 9C）. The number of upper jaw teeth increased rapidly to about 6 mm BL and exponentially thereafter with a maximum number of 84 at 17.7 mm BL.

Although the first lower jaw tooth was observed at 2.8 mm BL, the increase of number was slow up to 7 mm BL with a maximum number of six（Fig. 9D）. The number of lower jaw teeth increased exponentially up to about 13 mm BL with a maximum number of 50, and the in-

crease ratio became slow thereafter and varied from 40 to 70 in number.

Suspensorium: The smallest specimen of 2.0 mm BL possessed the palato-quadrate and hyo-mandibular-symplectic cartilages. The cartilaginous palatine was first observed at 2.6 mm BL. The quadrate, metapterygoid, symplectic and hyomandibular started ossifying at 5.9 mm BL, and the palatine at 6.5 mm BL. The bony ectopterygoid and endopterygoid were first observed at 4.1 mm BL and 8.0 mm BL, respectively.

Hyoid arch and branchiostegal rays: The hypohyal, cerato-epihyal, and interhyal cartilages were first observed at the smallest specimen of 2.0 mm BL. The interhyal, ceratohyal and epihyal started ossifying at 6.5 mm BL, and the hypohyal at 6.8 mm BL.

Three branchiostegal rays were first observed at 2.8 mm BL, and the adult complement of six rays was attained at 4.3 mm BL (Fig. 9E).

Opercular bones: A bony opercle appeared first at 2.0 mm BL, followed by the preopercle at 3.4 mm BL, subopercle at 3.8 mm BL and interopercle at 4.1 mm BL.

Pharyngeal teeth: One upper pharyngeal tooth was first discerned at 2.0 mm BL (Fig. 9F). The number of upper pharyngeal teeth increased and reached a maximum number of 137 at 17.7 mm BL. On the other hand, one lower pharyngeal tooth was first observed at 2.3 mm BL (Fig. 9G). The number increased and reached a maximum number of 70 at 14.8 mm BL.

Prevomer teeth: One prevomer tooth was observed in specimens from 8.0 to 12.9 mm BL (Fig. 9H). The second prevomer tooth appeared at 10.8 mm BL, and the number increased slowly with a maximum number of 12 at 21.1 mm BL.

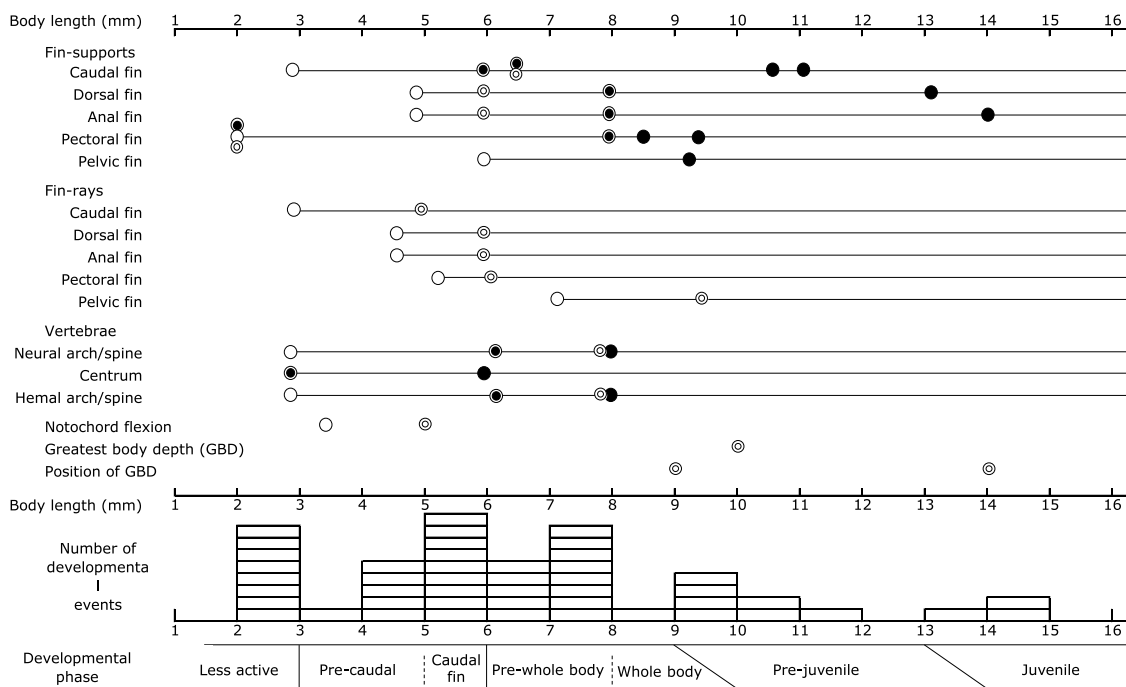## 4. Discussion
4.1 Developmental phases
4.1.1 Developmental phases of swimming function

Based on the development of swimming-related characters shown in Figure 10, the Japanese whiting larvae and juveniles were divided into the following five developmental phases.

The phase of less active swimming (from 2 mm BL to 3 mm BL): No swimming-related characters appeared, other than the pectoral fin elements such as the cleithrum, coraco-scapular cartilage and cartilaginous plate, which developed later into actinosts. No fin rays appeared, and all the fins were composed of fin-fold. Therefore, the larvae in this phase are considered to drift passively rather than to swim actively.

The phase of caudal fin propulsion (from 3 mm BL to 6 mm BL): This phase is divided into two sub-phases, pre-caudal and caudal fin propulsion sub-phases, at about 5 mm BL. In the former sub-phase, notochord end flexion started and was completed. Caudal fin supports started appearing, and the caudal fin rays started appearing and were completed in number. The hemal and neural arches and spines and the vertebral centra started appearing. The flexion of notochord end as well as the completion of caudal fin rays in number indicate that the beating of caudal fin produces weak propulsion (Kohno et al., 1983). In the latter sub-phase, on the other hand, the dorsal, anal and pectoral fin supports and rays started appearing and reached the adult complement, indicating that the body balance became stable (Gosline, 1971) and thus the beating ability of caudal fin would increase (Kohno and Sota, 1998).

The phase of whole body propulsion (from 6 mm BL to 9–10 mm BL): This phase is also divided into two sub-phases, pre-whole and whole body propulsion sub-phases, at about 8 mm BL.

Fig. 10 Schematic representation of the development of swimming-related characters with growth, showing the developmental phases in the Japanese whiting, *Sillago japonica*, collected from the inner Tokyo Bay. ○: cartilaginous elements and fin rays start appearing or notochord flexion begins; ◎: all cartilaginous elements appear, numbers of fin rays and vertebral elements and notochord flexion become complete, or flexion points of morphometric characters appear; ◉, bony elements start appearing, or cartilaginous elements start ossifying; ●: all cartilaginous elements start ossifying, or all bony elements start appearing. Developmental events are shown by boxes, and developmental phases are also shown in the bottom.

The vertebral centra were completed in number; therefore, the strong body axis and completed dorsal and anal fins allow larvae to swim powerfully by propagating the beat of the whole of the body posterior to generate propulsion (OMORI *et al.*, 1996). In addition, at about 8 mm BL, the neural and hemal arches and spines were completed in number and started ossifying, and all the dorsal and anal fin supports started ossifying. The completed dorsal and anal fin supports and rays prevent the larvae from rolling caused by whole-body beating (GOSLINE, 1971). The pectoral fin supports were also completed, and the pelvic fin support and rays appeared and were completed,

indicating that the specimens became a juvenile stage with possessing the completed, adult number of fin rays at 9.4 mm BL. The development of paired fins indicates the improvement of maneuverability (LAGLER *et al.*, 1977; MATSUOKA, 1987; NARISAWA *et al.*, 1997).

The phase of pre-juvenile swimming (from 9–10 mm BL to 13–14 mm BL): All bony elements appeared and all cartilaginous elements started ossifying in the caudal fin support. Flexion points occurred in the greatest body depth and its position; changes of the body depth and position are considered to be the improvement of swimming in fish (ALEEV, 1963).
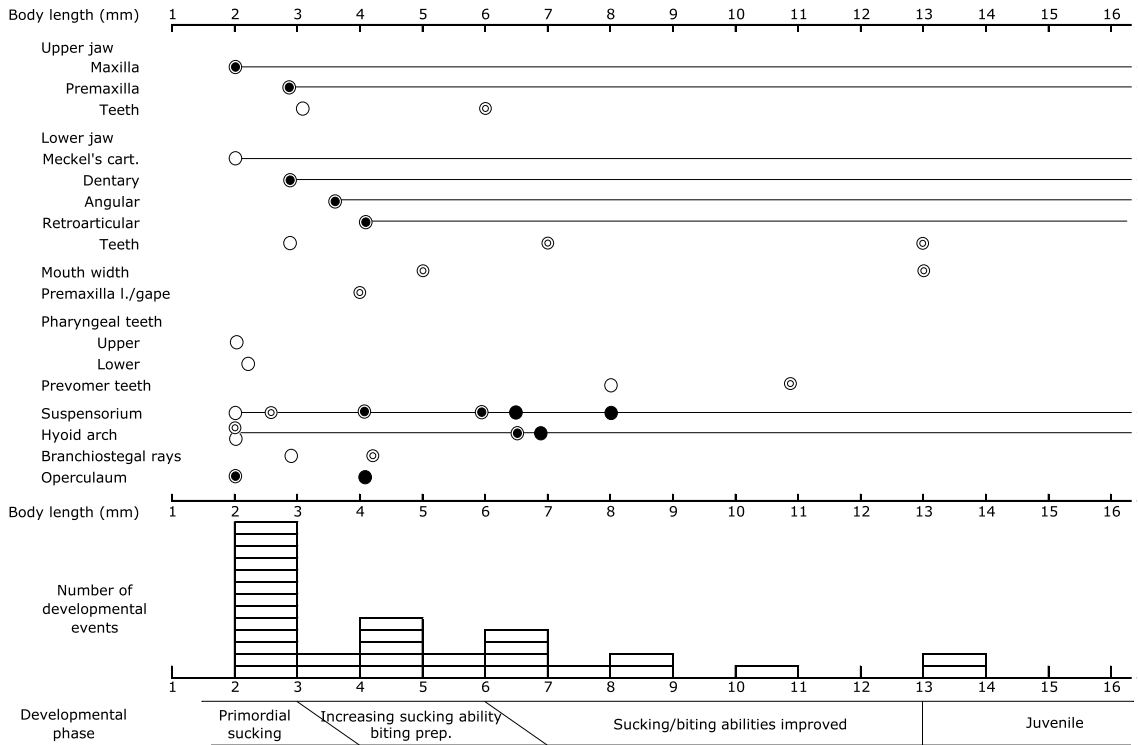
Body length (mm)　1　2　3　4　5　6　7　8　9　10　11　12　13　14　15　16

Upper jaw
　Maxilla
　Premaxilla
　Teeth
Lower jaw
　Meckel's cart.
　Dentary
　Angular
　Retroarticular
　Teeth
Mouth width
Premaxilla l./gape
Pharyngeal teeth
　Upper
　Lower
Prevomer teeth
Suspensorium
Hyoid arch
Branchiostegal rays
Operculaum

Body length (mm)　1　2　3　4　5　6　7　8　9　10　11　12　13　14　15　16

Number of developmental events

Developmental phase　｜ Primordial sucking ｜ Increasing sucking ability biting prep. ｜ Sucking/biting abilities improved ｜ Juvenile

Fig. 11 Schematic representation of the development of feeding-related characters with growth, showing the developmental phases in the Japanese whiting, *Sillago japonica*, collected from the inner Tokyo Bay. ○: cartilaginous elements and fin rays start appearing or notochord flexion begins; ◎: all cartilaginous elements appear, numbers of fin rays and vertebral elements and notochord flexion become complete, or flexion points of morphometric characters appear; ◉, bony elements start appearing, or cartilaginous elements start ossifying; ●: all cartilaginous elements start ossifying, or all bony elements start appearing. Developmental events are shown by boxes, and developmental phases are also shown in the bottom.

The phase of functional, juvenile swimming (*over 13–14 mm BL*): All characters concerning swimming function became complete in number and started ossifying, and the position of greatest body depth became stable. Therefore, juveniles larger than 13–14 mm BL were considered to have acquired the functional, juvenile swimming mode.

4.1.2 Developmental phases of feeding function

Based on the development of feeding-related characters shown in Figure 11, the Japanese whiting larvae and juveniles were divided into the following four developmental phases.

The phase of primordial sucking (*from 2 mm BL to 3–4 mm BL*): The oral cavity was enclosed by the maxilla, Meckel's cartilage, a part of suspensorium and hyoid arch, indicating that the feeding mode is sucking. However, these elements, other than the small bony maxilla, are cartilaginous, and thus negative pressure for sucking is considered to be low (e.g. KOHNO *et al.*, 1997).

The phase of increasing sucking ability and biting preparation (*from 3–4 mm BL to 6–7 mm*

BL): The gape elements of the premaxilla, dentary and angular started appearing, indicating that gape opening and closing ability increase (SHINAGAWA *et al.*, 2002). In addition, the ossification of suspensorium and appearance of branchiostegal rays, opercular bones and retroarticular would increase the sucking ability (TAMURA *et al.*, 2013). Although the number is low, the upper and lower jaw and pharyngeal teeth started appearing in this phase. The functions of the jaw and pharyngeal teeth are to bite/capture and to propel acquired food organisms to the digestive tract, respectively (GOSLINE, 1971). Therefore, this phase is also recognized as a phase of biting preparation.

The phase of sucking/biting abilities improved (from 6–7 mm BL to 13 mm BL): All characters concerning feeding function, except for the number of jaw, pharyngeal and vomer teeth, became complete not only in number but ossification. The larvae/juveniles of this stage are considered to improve their feeding abilities.

The phase of functional, juvenile feeding (over 13 mm BL): The number of lower jaw teeth became stable, and the flexion point of mouth width, which determines the size of food organisms (HUNTER, 1981), was noticed. Therefore, the functional, juvenile feeding mode was considered to be acquired in juveniles over 13 mm BL.

4.2. Habitat shifts corroborated by functional development

The smallest Japanese whiting larva collected in this study was 2.0 mm BL, in which the yolk was completely absorbed. OOZEKI *et al.* (1992) reported that a newly hatched larva was 1.2 mm BL and the yolk was completely absorbed at 2.5 mm BL of five days after hatching. Considering the lack of yolk and the shrinkage of body size as pointed out by OOZEKI *et al.* (1992), the smallest larva of 2.0 mm BL collected in this study would

be older than five days after hatching. Although the size of larvae collected from the offshore water in this study ranged from 2.0 to 8.5 mm BL, the dominant size class was 3.0–3.9 and 4.0–4.9 mm BL (Fig. 4), which occupied 33.3 and 30.0 % of the total number of offshore specimens. Swimming and feeding modes of the dominant larvae were the pre-caudal propulsion and sucking ability increasing/biting preparation, and thus the larvae occurred in the offshore water in this study do not swim actively but drift passively or swim weakly nor feed actively. The dominant size of the offshore specimens would be attained by one to two weeks after hatching, according to the results of OOZEKI *et al.* (1992).

The larvae > 6 mm BL started appearing on tidal flats, and the number increased after 8 mm BL and reached to a peak of occurrence at the 14.0–14.9 mm BL size class (Fig. 4). During the size from 6 to 14 mm BL, the swimming mode progressed from pre-whole body propulsion to pre-juvenile phases, which were divided at about 10 mm BL (Fig 10). In the former phase, which would correspond to two to three weeks after hatching (OOZEKI *et al.*, 1992), the larvae are considered to migrate shoreward by not strong but spontaneous swimming as well as by utilizing water currents, and they became juveniles morphologically at 9.4 mm BL by the completion in number of all fin rays. In the latter, pre-juvenile phase, the increase of individual number on tidal flats was accounted by the active shoreward migration supported by the improvement of swimming ability. On the other hand, the feeding abilities of both the sucking and biting were improved during the size from 6 to 14 mm BL (Fig. 11). ARAYAMA *et al.* (2003) reported that the main food of the species between 7.0 and 13.9 mm BL was calanoid copepods, and after 14 mm BL polychaet larvae were added; this change of feeding pattern is in accord with the change of

swimming and feeding modes revealed in this study.

The number of juveniles > 15 mm BL decreased gradually on tidal flats, and those > ca. 30 mm BL were absent besides exceptionally large individuals of 33, 43 and 49 mm BL (Fig. 4). KRÜCK *et al.* (2009) suggested a possibility that a niche shift would occur in sillaginid fishes > 20 mm BL in Moreton Bay, Australia, which more or less agrees with our results of the disappearance pattern from tidal flats. Although a habitat shift occurred from intertidal pools to adjacent subtidal waters in Moreton Bay (KRÜCK *et al.*, 2009), no habitats after the tidal flats which corresponding to the subtidal waters in Moreton Bay could be detected for the Japanese whiting in the innermost Tokyo Bay. ARAYAMA *et al.* (2003) indicated that, in Tateyama Bay of the outer Tokyo Bay, an offshore area within 100 m from the shoreline at the depth < 1 m is an important nursery area for the Japanese whiting and that the occurrence of larvae/juveniles in the shoreline area corresponding to the tidal flats in this study would be accidental. However in the innermost Tokyo Bay, we could not find nursery areas corresponding to the offshore area of ARAYAMA *et al.* (2003); those > ca. 30 mm BL in the innermost Tokyo Bay are most likely to move into deeper waters.

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Taxonomical review of *Auxis* (Scombridae, Pisces) larvae using collections around Tosa Bay, Japan

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Abstract: Larvae of *Auxis* collected around Tosa Bay from May 2002 to May 2018 could be distinguished into two types primarily by the pigmentation patterns on the caudal peduncle. Type-A *Auxis* larvae possess a row of pigmentation along the midlateral line in all larval stages, while type-B does not. Little morphometric differentiation was found until the flexion stage in both types, but at the postflexion type-A showed significantly larger head [36.8% BL(mean)], larger mouth (24.1%), shorter vent to anal-fin length (17.7%) and deeper body (27.8%) than type-B (34.8, 21.5, 19.0, 25.9%, respectively). These observed differences indicate the validity of the pigmentation row in distinguishing *Auxis* larvae. Between the two types, type-B larvae (n = 795) were more abundant than type-A (n = 21) in Tosa Bay. Based on this distribution pattern and shallower body depth, type-B larvae could be considered as *A. rochei* and type-A with a deeper body as *A. thazard*.

Keywords : Auxis larvae, pigmentation and morphometry, Tosa Bay

1. Introduction

Auxis is a commercially important fish with widespread distribution in tropical to temperate waters (Collete and Nauen, 1983). It is represented by four species, *A. brachydorax, A. eudorax, A. rochei* and *A. thazard* (Fricke *et al.*, 2018). The latter two species are cosmopolitan in distribution, while the former two species have been recorded only in the eastern Pacific and are previously considered as subspecies of *A. thazard* and *A. rochei*, respectively (Collette and Aadland, 1996). Around Japanese waters, both *A. rochei* and *A. thazard* are widely distributed, with the former dominating fisheries catches

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throughout the year (Hotta, 1955; Okachi, 1958; Mohri *et al.*, 2016), half of which are landed from Tosa Bay (Ochiai and Tanaka, 1998; Niiya, 2001). This demonstrates the importance of Tosa Bay in the reproduction of pelagic fishes in southwestern Japan (Kinoshita, 2006).

Global capture production of *Auxis* from 2010–2015 showed a general increasing trend, with an annual average of ca. 457 kt (FAO, 2018a). However, in Japan *Auxis* capture production continue to decline from ca. 29 kt in 2010 to ca. 16 kt in 2015 (FAO, 2018b). To manage fisheries resources sustainably, precise identification (Fischer, 2013) and information on the early life histories that has considerable influence on population dynamics (Sponaugle and Cowen, 1997) should be acquired. Currently, identification of

the larvae of the two cosmopolitan *Auxis* species is still problematic. MATSUMOTO (1959) classified *Auxis* larvae into two types using pigmentation patterns of the caudal peduncle region, and JONES (1963) speculated that these types I and II may be *A. thazard* and *A. rochei*, respectively. However, because of the lack of detailed morphometric examinations, both works are inconclusive.

There is little available information on the early life history of *Auxis* in Japan. Most of the information are limited to collection records based on ichthyoplankton studies (YOKOTA *et al.*, 1961; YABE and UEYANAGI, 1962; HATTORI, 1964; MATSUDA, 1969; FUKUDA, 1984; FUNAKOSHI, 1993; ZHONG, 2002). Artificially reared larvae and juveniles of both *Auxis* species were reported in HARADA *et al.* (1973a, b), but their papers never describe their ontogeny. To date, only NISHIKAWA (2014) described an uncertain species of *Auxis*, which may probably be any of the two types observed by MATSUMOTO (1959). This study aims to differentiate the early developmental stages of *Auxis* larvae collected around Tosa Bay, Japan based on pigmentation patterns and morphometric trends. Detailed descriptions of pigmentation and morphometric patterns are also provided to determine which characters are most useful in separating *Auxis* even at early developmental stages.

2. Materials and methods

Fish larvae were collected in waters of Tosa Bay (32° 42″-33° 25″ N, 132° 52″-133° 38″ E) from May 2002 to May 2018, primarily by towing obliquely from near the bottom to the surface with a larva net (1.3 m mouth diameter with 0.5 mm mesh aperture) and a modified IKMT (1.5 m² mouth opening with 2 mm and 0.5 mm mesh apertures in the anterior part and cod end, respectively). All samples collected were preserved in 10% formalin solution. Fishes were

immediately sorted and transferred to 80% ethanol. *Auxis* larvae were identified following MATSUMOTO (1959), NISHIKAWA and RIMMER (1987) and NISHIKAWA (2014). Larvae of *Auxis* can be distinguished from other scombrids containing the same number of myomeres (39) such as *Thunnus, Euthynnus* and *Gymnosarda* based on the pigmentation patterns on the caudal peduncle, chleithral symphysis, front of the anus and tip of the lower jaw.

After identification, the body lengths (BL: notochord length in preflexion and flexion larvae, and standard length in postflexion larvae) and other various measurements such as eye diameter, body depth, snout, upper jaw, pre-anal, head and vent to anal-fin (VAFL) lengths were made following LEIS and CARSON-EWART (2000) by developmental stages (KENDALL *et al.*, 1984). A total of 642 preflexion (2.3–4.6 mm BL), 140 flexion (4.7–7.1 mm) and 34 postflexion (5.5–7.9 mm) larvae of *Auxis* were collected and representative samples were used to describe the different developmental stages.

Morphometric data were evaluated for heterogeneity of variances using ANCOVA. A representative series of specimens used in this study were deposited in the Usa Institute of Marine Biology, Kochi University (UKU-449000–449005).

3. Results
Types of larvae

Specimens were classified into two types primarily using pigmentation patterns. Type-A specimens possessed a distinct row of melanophores along the midlateral line of the caudal peduncle, while type-B did not. Both types occurred almost simultaneously in spring to autumn, with type-B larvae outnumbering type-A on all occasions (Fig. 1). A total of three preflexion (4.1–4.3 mm BL), three flexion (4.8–5.5 mm) and 15 postflexion larvae (5.5–7.9 mm) of type-A,
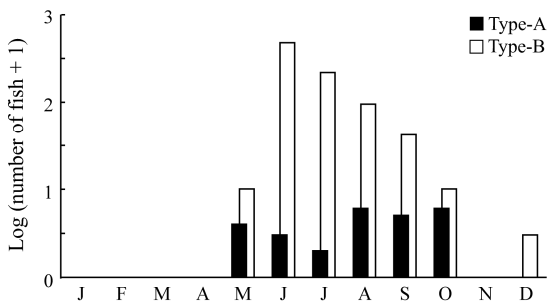
Fig. 1 Seasonal abundance of types -A and -B *Auxis* larvae collected in Tosa Bay from May 2002 to May 2018.

while 639 preflexion (2.3–4.6 mm), 137 flexion (4.7–7.1 mm) and 19 postflexion larvae (5.6–7.6 mm) of type-B were collected (Fig. 2).

General morphology

Both types containing 39 myomeres are laterally compressed with an elongate body tapering gradually towards the caudal end. The abdominal sac is triangular and protrudes ventrally be-low the body outline. In both types, the pre-anal (ca. 40–48% BL), head (ca. 26–37%), upper jaw (ca. 16–24%) and snout (ca. 7–14%) lengths and body depth (ca. 24–28%) increase with body length (Fig. 3a, b, d). Eye diameter hardly changes with BL (ca. 11–12%) (Fig. 3e), while the VAFL becomes shorter (ca. 22–17%) (Fig. 3c) from preflexion to postflexion. However, at the postflexion stage, significant differences between the two types were observed, with type-A having a larger head [36.8% BL vs 34.8% (means) in type-B, $p < 0.05$], longer upper jaw (24.1% vs 21.5%, $p < 0.05$), shorter VAFL (17.7% vs 19.0%, $p < 0.01$) and deeper body (27.8% vs 25.9%, $p < 0.01$) than type-B (Fig. 3f, g, h). Correspondingly, the snout and pre-anal body length in type-A (14% and 48%) are also longer than type-B (13% and 47%, respectively), but these were not significant.

Fin formation

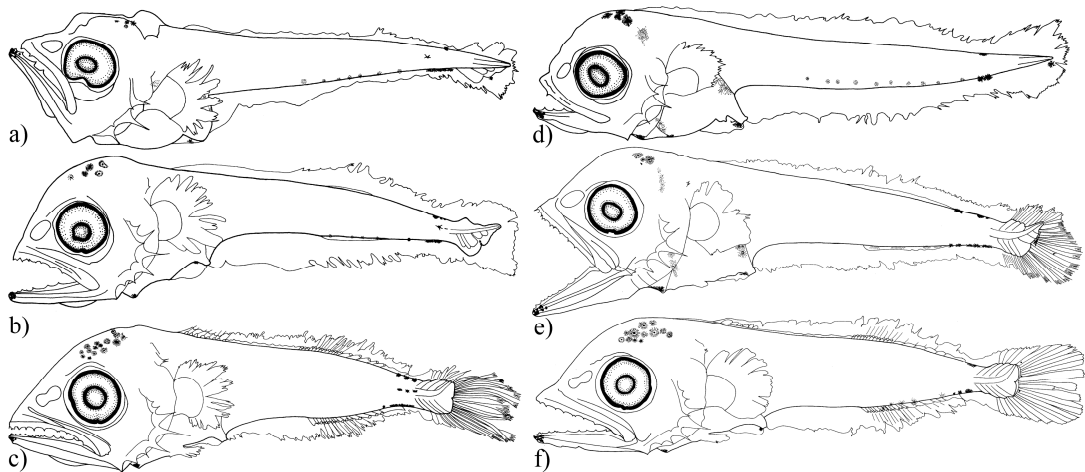Notochord flexion begins at 4.8 mm BL in

Fig. 2 Developmental stages of types -A (a-c) and -B (d-f) *Auxis* larvae from Tosa Bay. (a) 4.3 mm BL preflexion larva (UKU-449000); (b) 5.4 mm BL flexion larva (UKU-449001); (c) 6.8 mm BL postflexion larva (UKU-449002); (d) 5.0 mm BL preflexion larva (UKU-449003); e 6.9 mm BL flexion larva (UKU-449004); (f) 7.5 mm BL postflexion larva (UKU-449005). Note: Fig. 2a was derived from the right side body of the larva due to damage on the left side.

type-A and at 4.7–5.2 mm in type-B, and is completed at 5.5 and 6.9 mm, respectively (Fig. 2e). The hypurals start to appear in late preflexion larvae measuring 4.3 mm in type-A (Fig. 2a) and in 4.6–5.2 mm in type-B, with incipient rays formed subsequently. The pelvic bud occurs in 4.8 mm flexion larva in type-A and in 5.1 mm flexion larvae in type-B, with rays starting to develop at 6.5 and 7 mm postflexion larvae, respectively. The second dorsal- and anal-fin anlagen first appear in 4.8 mm flexion larvae of type-A and in 5.2 mm flexion larvae of type-B, and their incipient fin rays begin to differentiate in 5.5 and 6 mm flexion larvae, respectively. The first dorsal-fin anlagen are found in late flexion larvae measuring 5.5 mm in type-A and 7 mm in type-B, with incipient spines starting to form in 6.6 and 7.3 mm postflexion larvae, respectively. The 7.9 mm postflexion larva of type-A was the largest in both types, and showed full complements of first dorsal (XI), second dorsal (11 + 7 finlets), anal (11 + 7 finlets), pelvic (I + 5) and caudal (9 + 8) fins (pectoral fin, unkown due to damage).

Head spination and dentition

In both types, two and three spines are initially present on the inner and outer preopercle, with the outer spine at the angle being the longest (Fig 2a, d). The number of inner and outer spines increase gradually to three and seven, respectively, by postflexion stage in both types (Fig. 2c, f). One small spine starts to form on the posttemporal in 5.4 mm BL flexion larvae (Fig. 2b), increasing to two in ca. 6 mm flexion larvae in both types (Fig. 2c, 2e). The small and conical teeth are already present in both jaws in the smallest larvae at 4.1 mm in type-A and 2.3 mm in type-B, gradually increasing their number with development thereafter (Fig. 2).

Pigmentation

Three distinct rows of melanophores (middorsal, midlateral and midventral) are present on the caudal peduncle in type-A (Fig. 2a-c), while one or two rows only in type-B, along the midventral and or middorsal (Fig. 2d-f), which is sometimes absent in preflexion and flexion larvae. The rows on the caudal peduncle become denser with growth in both types, and the three rows of type-A form a transverse band (Fig. 2a-c). The internal melanophores arranged along the anal-fin anlagen are more numerous in preflexion type-B larvae (6–13) than in type-A (5–8) (Fig. 2a, c), and their number decreased, although variable, to 1–5 in type-A (Fig. 2c) and 3–6 in type-B at postflexion (Fig. 2f). Small melanophores at the tip of the lower jaw and large branched melanophores over the head are present in all stages in both types, becoming more obvious with growth (Fig. 2). Melanophores on the triangular abdominal sac are internally developed, being heavier along the anterior and dorsal surfaces from flexion larvae (Fig. 2). A conspicuous melanophore at the cleithral symphysis (Fig. 2b-f) is present in most specimens, but sometimes absent in type-A preflexion larvae (Fig. 2a) and in any stage of type-B larvae. A single melanophore just in front the tip of the anus and/or the anterior finfold (Fig. 2a, b, d, e, f) irregularly appears in any stage in both types.

4. Discussion

The midlateral row of melanophores on the caudal peduncle is the most consistent feature distinguishing all larval stages of type-A from type-B. Both types closely resemble MATSUMOTO'S (1959) types I and II larvae, respectively from unspecified waters of the Pacific, Atlantic and Indian Oceans, based on pigmentation patterns. Although MATSUMOTO (1959) mentioned the extreme inconsistency of the midlateral pigments
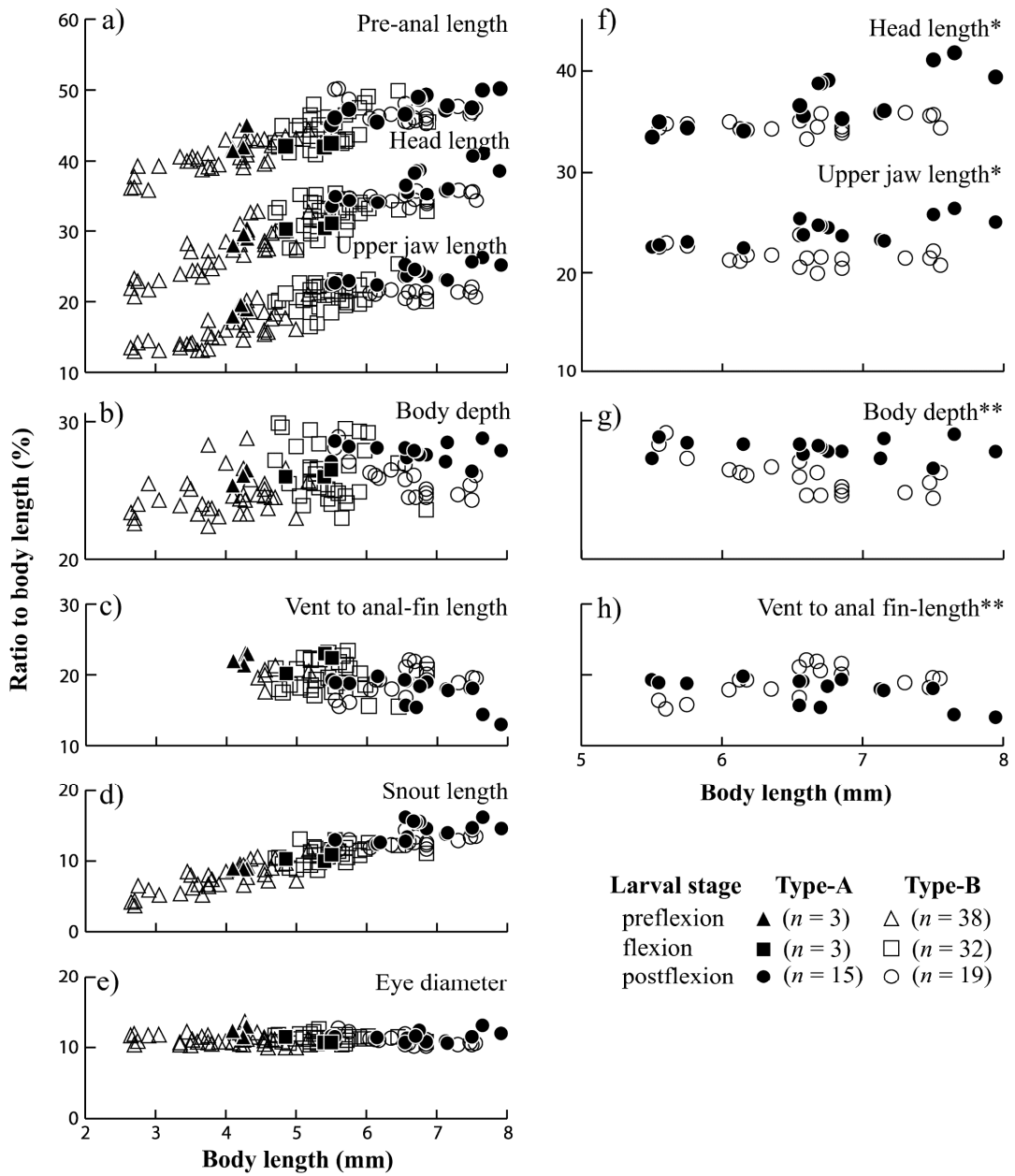
Fig. 3 Changes in the ratio of the different morphometrics measured to body length of *Auxis* types -A and -B larvae covering all larval stages (left: a-e), and upon attaining postflexion stage (right: f-h). ** and * indicate significant differences between the two types with *p* value < 0.01 and < 0.05, respectively.

in type I larvae（a row of 1–5 melonophores on one side of the body but absent on the other side on the same larvae）, our type-A specimens have the pigments on both sides, except for the 4.3 mm BL preflexion larva (Fig. 2a). This specimen had a damaged caudal peduncle on the other side, hence, the presence or absence of the pigment row is uncertain. Nevertheless, we are convinced that this specimen possessed the pigment because the other two preflexion type-A larvae（4.1 and 4.3 mm BL, with deformed bodies）have the pigment row on both sides.

The morphological features of both types -A and -B are very similar in the early larval stages. Differences are recognizable only at the postflexion stage, with type-A larvae showing a larger head, larger mouth, shorter VAFL and deeper body than type-B（Fig. 3）. These results indicate the validity of the pigmentation row on the midlateral line in typing the entire larval stages of *Auxi*s, probably until the juvenile stage.

The body depths of juvenile and adult *A. rochei* are shallower than in *A. thazard*（COLLETTE and AADLAND, 1996; NAKABO and DOIUCHI, 2013）. In Tosa Bay, *A. rochei* are captured more abundantly than *A. thazard*（OCHIAI and TANAKA, 1998; NIIYA, 2011）. In this study, the shallower-bodied type-B larvae predominated the deeper-bodied type-A larvae. Based on these facts, type-B larvae can be considered as *A. rochei* and type-A larvae as *A. thazard*. Our opinion corroborates with JONE'S（1963）speculations based on a limited morphometric examination（eight specimens）that the stouter type of *Auxis* larvae from Indian waters may be a *A. thazard* [= type I of MATSUMOTO（1959）] and the less stout or elongate type may be *A. rochei* [= type II of MATSUMOTO（1959）]. Furthermore, the photographs, although unclear, of the artificially reared preflexion larvae of *A. thazard* and *A. rochei* have three and two rows of pigmentation on the caudal peduncle, respectively（HARADA *et al.*, 1973b, a）. Accordingly, based on the results of this study, the three postflexion *Auxis* larvae observed in NISHIKAWA（2014）can be identified as *A. thazard*, but the smallest preflexion larva is not *Auxis* because of the absence of pigmentation rows on the midventral, middorsal and/or midlateral lines of the caudal peduncle which are distinguishing characteristics of *Auxis* even in early preflexion larvae. This preflexion specimen is probably *Euthynnus*（NISHIKAWA, 2014）, which has 1–3 pigment spots on the ventral edge of the tail and shares the same characters with *Auxis*; such as 39 myomeres, strong preopercular spines and pigmentations at the tip of the lower jaw, cleithral symphysis and tip of anus. In the near future, molecular studies examining the two types of *Auxis* larvae should be conducted to clarify their identifications.

Acknowledgements

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Measuring burst movements of smallmouth bass (*Micropterus dolomieu*) in Lake Kizaki, Japan, using micro-acceleration data loggers

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Abstract: This study used micro-acceleration data loggers to measure burst movements, such as feeding behavior, of smallmouth bass (*Micropterus dolomieu*). Data loggers were attached to the dorsal side of seven bass released into Lake Kizaki, Japan, during summer 2007–2008. From 220.7 total hours of data, the burst movement rate was 0.7 ± 0.3 events/hour (mean ± s.d.) (range: 0.4–1.1 events/hour). All bass showed burst movements during both daytime and nighttime, but four fish had higher event rates during the day. For two individuals, the mean event depth was significantly deeper during the daytime than the nighttime.

Keywords : *invasions, fish behavior, bio-logging, micro-acceleration data logger*

Introduction

Smallmouth bass (*Micropterus dolomieu*) are freshwater fish native to North America that were introduced to Japanese lakes in the mid-1990s and have been successfully reproducing since then (Iguchi *et al.*, 2001). The introduction of this competitive species likely has serious consequences for native species (Iguchi *et al.*, 2004).

Bio-logging tools have proven useful for behavioral ecology research, specifically to assess behavior in marine mammals, seabirds, and other free-living species that are difficult to study (Kato *et al.*, 1996; Suzuki *et al.*, 2009; Naito *et al.*, 2010). Micro-accelerometer tags are efficient tools to remotely quantify rates of behaviors such as resting, swimming, or migrating, and can

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Table 1. Logger data of burst movements of smallmouth bass in Lake Kizaki. Data were collected from 130.3 nighttime and 90.4 daytime hours.

ID	Capture date	TL (cm)	BW (g)	Water temp. (℃)	Daytime N	Daytime RT (h)	Daytime Rate	Nighttime N	Nighttime RT (h)	Nighttime Rate	Total N	Total RT (h)	Total Rate
F	2007/5/20	34.1	640	14.3 ± 0.1	14	13.7	1.0	5	9.7	0.5	19	23.4	0.8
I	2007/8/10	42.1	–	26.3 ± 0.3	18	27.5	0.7	12	20.2	0.6	30	47.7	0.6
Q	2008/6/12	40.4	–	18.8 ± 0.2	12	14.5	0.8	5	9.2	0.5	17	23.6	0.7
R	2008/6/12	40.3	1080	19.0 ± 0.1	5	14.3	0.4	4	9.2	0.4	9	23.5	0.4
S	2008/6/16	38.2	–	20.2 ± 0.5	6	14.6	0.4	5	9.2	0.6	11	23.7	0.5
U	2008/8/13	38.3	–	26.5 ± 0.2	15	26.5	0.6	13	20.5	0.6	28	47.0	0.6
X	2008/8/24	40.1	–	25.0 ± 0.3	23	19.2	1.2	13	12.4	1.1	36	31.6	1.1
Mean ± s.d.		39.1 ± 2.6	–	21.4 ± 0.2	13.3 ± 6.4	18.6 ± 6.0	0.7 ± 0.3	8.1 ± 4.3	12.9 ± 5.2	0.6 ± 0.2	21.4 ± 10.2	31.5 ± 11.2	0.7 ± 0.3

TL: total length, BW: body weight, N: number of burst movements, RT: record time, Rate: burst movement rate per hour, -: no data

be used to estimate activity and energy budgets (FØRE *et al.*, 2011; ALABSI *et al.*, 2011; BROELL *et al.*, 2013). These devices allow the measurement of swimming intensity and active events (AOKI *et al.*, 2012), which can be used to estimate the quantity of food eaten (TANOUE *et al.*, 2012) and indicate the ecology of fish species.

This study explored the activity of smallmouth bass and investigated the potential of biologging devices for acquiring data on their burst movements such as feeding behavior. We also collected data on spatiotemporal swimming behavior of smallmouth bass to extrapolate their potential threats to native fish populations in Lake Kizaki.

Materials and methods

Smallmouth bass were caught by lure fishing from Lake Kizaki (36° 32–34'N, 137° 49–50'E, shoreline length: 7 km, surface area: 1.4 km^2, volume: 0.02 km^3, height: 764 m, maximum water depth: 29.5 m, transparency: 4 m,) in Nagano Prefecture, Japan, during the summers of 2007–2008. In May, nests of smallmouth bass were visually located. Individuals with IDs A-I were caught in in 2007, and IDs J-X were caught in 2008.

They were housed in a fish cage (3 × 3 × 1 m) in the lake to identify burst movements including feeding events via direct visual observation and video camera put from the cage side. Individuals (n = 7) were tagged with a micro-acceleration data logger M190–D2GT (Little Leonardo Co., Tokyo, Japan) to measure burst movements and other variables. Less than 24 h after the logger was tagged, three or five live loach (*Misgurnus* spp.), goldfish (*Carassius auratus*), and Japanese smelt (*Hypomesus nipponensis*) were introduced to the cage to allow the tagged fish to feed *ad libitum*. After the caged experiments, the tagged fish (n = 2 in 2007, n = 5 in 2008) were released into Lake Kizaki (Table 1).

The data loggers (53 mm × 15 mm, 6 g in water) measured depth and temperature in 1 s intervals, and both static and dynamic acceleration along the lateral 'sway' and longitudinal 'surge' axes at 32 Hz. A soft nylon mesh (6 × 4 cm) was sewed onto the dorsal side of each fish using biodegradable thread made of polyglycolic acid (Matsuda Medical Technology Co., Tokyo, Japan). The data logger was wrapped in copolymer foam to keep it slight positive buoyancy in the water (KOMATSU *et al.*, 2011), and was attached to the nylon mesh with plastic bands. Data loggers had an automatic scheduled release system included VHF radio transmitter to detach from the nylon mesh and float to the surface (WATANABE *et al.*, 2008), where they were

Table 2. Activity patterns obtained by the data logger of smallmouth bass in a fish cage

Types of behavior	Criteria		
	High-pass filtering the swaying acceleration (m/s^2)	Beat frequency (Hz)	Change in body angles (degrees)
Feeding	$\geqq 2.0$	$\geqq 3.0$	$\geqq 20$
Escaping	$\geqq 1.0$	$\geqq 2.5$	
Swimming	$\geqq 0.3$	$\geqq 1.5$	
Resting	< 0.3	< 1.5	

retrieved by the signal. One of the loggers tagged to nesting individuals (F) was detached in the same nest where the fish was caught.

Data were downloaded from the data loggers and analyzed using Igor Pro (v.6.0 J, WaveMetricks, Lake Oswego, OR, USA) and Igor Filtering Design Laboratory (IFDL: v. 4, WaveMetrics). Ethographer v. 1. 2 was used to detect specific waveforms among the large dataset of acceleration records (Sakamoto *et al.*, 2009). Power spectral densities (PSD) were calculated from swaying acceleration records from loggers to determine the dominant stroke cycle frequency using fast Fourier transformation. Tail beats were derived by high-pass filtering the swaying acceleration (Tanaka *et al.*, 2001). The body angle was extracted by low-pass filtering the surge acceleration. To remove higher frequency acceleration caused by tail beats, a low-pass filter was applied, with the threshold being the predominant frequency of tail beats to surging acceleration.

Results
Caged experiments

There were no observed differences in behavior between tagged and untagged fish in the cage 1 h after tagging. During the daytime, fish alternated between slow and rapid (burst) swimming events that characterize chase and predation behaviors. During feeding events, 95 % of high-pass filtering the swaying accelerations were more than 2 m/s^2, beat frequencies were more than 3 Hz, and changes in body angles were more than 20 degrees based on the acceleration waveforms measured using the logger (Table 2). As such, burst movements were defined as high-pass filtering the swaying acceleration $\geqq 2$ m/s^2, beat frequency $\geqq 3$ Hz, and changes in body angle $\geqq 20$ degrees in this study.

Field experiments

All loggers fitted to free-swimming fish were retrieved, and 220.7 data hours were collected (Table 1). The bass were more active in August (0.8 ± 0.3 burst movements per hour (mean ± s.d.)) than in June (0.5 ± 0.2). On average, burst movements occurred 0.7 ± 0.3 times per hour (range: 0.4–1.1; Table 1). All fish appeared to exhibit burst movements during both daytime and nighttime. The fish often swam before and after burst movements during the day but were inactive at night (Fig. 1). Four individuals (F, I, Q and X) showed a significantly higher rate of burst movements during the day than at night (Table 1). Two individuals (F and X) showed burst movements at a mean depth that was significantly deeper during the day than at night (*t*-test, $p < 0.01$). There were no significant differences among other individuals (Fig. 2).
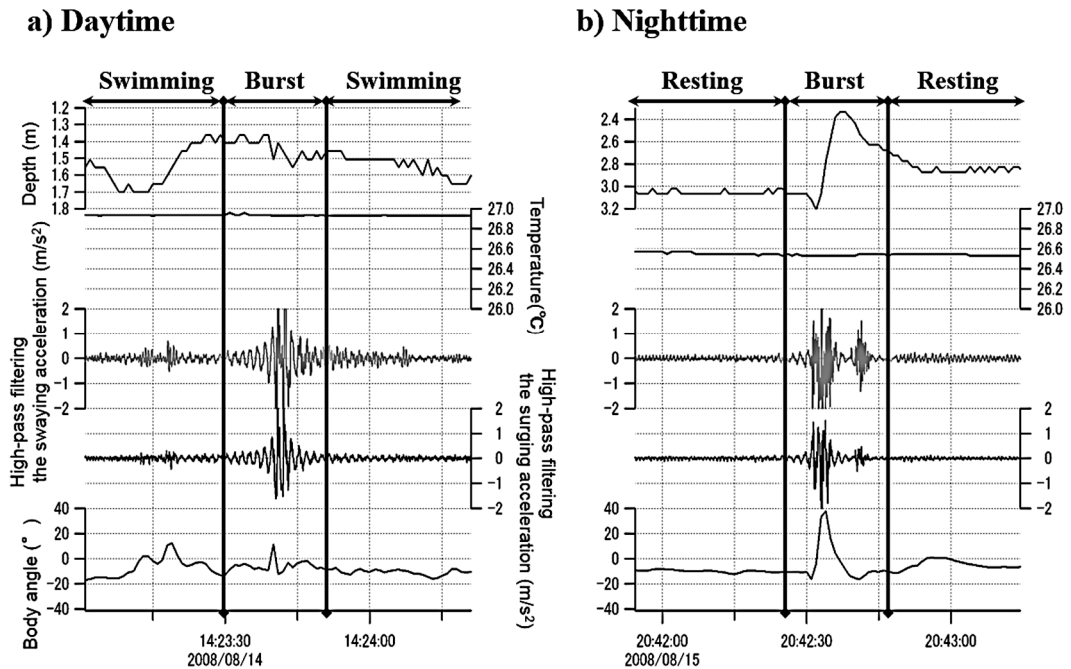
a) Daytime

b) Nighttime

Fig. 1   Comparison of one fish's (ID: U) burst movements associated with swimming and resting be-
haviors between (a) daytime and (b) nighttime in Lake Kizaki.

Discussion

Micro-acceleration data loggers enabled us to monitor the swimming behavior and activity patterns of introduced smallmouth bass in Lake Kizaki. Smallmouth bass are generally diurnal, often inactive at night except during spawning season (EMERY et al., 1973). The fish in our study were also more active during the day while in cages and free swimming (Fig. 1).

Smallmouth bass begin spawning once water temperatures exceed 14°C (RIDGWAY et al., 1991). According to AZUMA and MOTOMURA (1998) a spawning fish is greater than 20 cm in length, which may be reached 1–2 years after hatching. In May, we caught nesting individual (F) that was more than 20 cm in length. After being tagged and released, the individual returned to the nest and displayed burst movements at 14.3 ± 0.1°C. These bursts may be indicative of defense behavior, as smallmouth bass defend their eggs both during the day and at night (SCOTT and NICHOLAS, 1991).

Introduced smallmouth bass can alter the habitat and reduce the abundance of many small-bodied species in freshwater environments (MACRAE et al., 2001; JACKSON., 2002). Our study reveals the significant role that data-logging devices can play in researching fish behavior. Based on the behavior recorded in this study, we hypothesize that smallmouth bass display opportunistic and aggressive behaviors, and may act as competitors to other predators and stressors to small fish populations in Lake Kizaki. Future research should utilize micro-acceleration data loggers to study prey items and their capture, coupled with examinations of stomach contents.
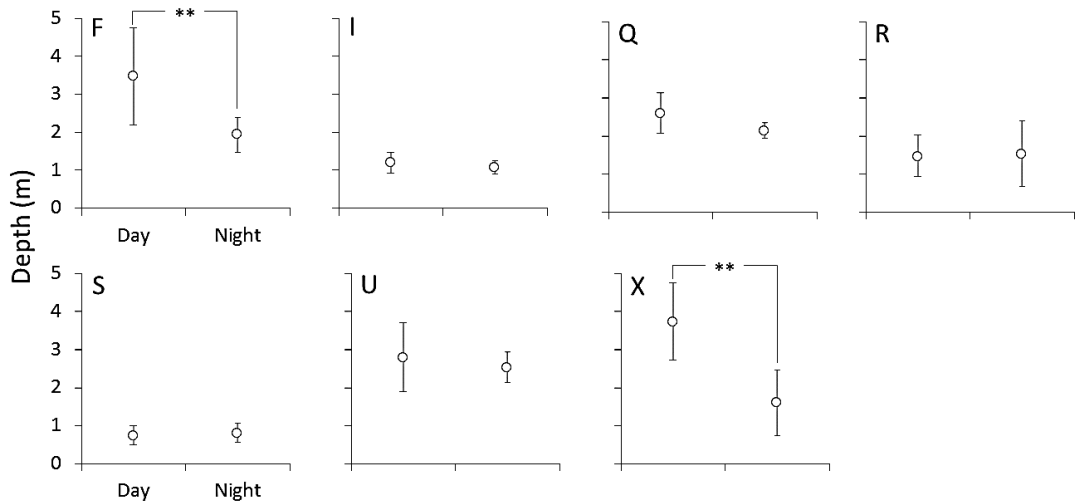
Fig. 2 Comparison of burst movement depth between daytime and nighttime in Lake Kizaki. Circles indicate mean. Error bars indicate standard deviation. Asterisks indicate significative difference between day and night (*t*-test results, $p < 0.01$).

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