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光を用いた魚類の行動制御（総説）

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Behavioral control of fish using light（A review）

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Abstract: Previous studies have reported that the use of light is effective for fishing, and specific wavelength light and aquarium colors are effective for control maturity, growth and survival of fish. Thus, the use of light in fishing and aquaculture has a long history. In the current study, we reviewed previous findings regarding the relationship between fish visual function, the ocean light environment, and responses of fish to light. We examined the effects and problems associated with the impacts of artificial light on fish behavior. The findings highlight the importance of understanding the ecology of adult fish during development from larvae, as well as visual function, behavioral responses to light, and physiological responses of fish at each developmental stage. Clarifying these issues is necessary for elucidating the most effective light conditions for fishery, seed production and aquaculture.

Keywords: *Behavioral control, Light, Light intensity, Photoperiod, Spectrum*

1. はじめに

海域や屋内で光を利用し，海洋生物の行動を制御して漁業や飼育（種苗生産，養殖）を行ってきた歴史は古い。漁業では，漁火（いさりび）等を用いたことが万葉集に記載されている（稲田ほか, 2010）。日本の集魚灯漁業は，1950 年代以降の照明機材の発達により，高出力の光源が開発され（稲田・小倉，1988），漁獲効率が増大した。近年，さんま棒受網漁業では指向性が高く，特定波長の光を発する LED（発光ダイオード）灯の利用が拡大している。

一方，屋内施設での飼育には，白熱灯，水銀灯や蛍光灯が利用されてきた。これらの照明を用いてこれまで，照度（DOWNING and LITVAK, 1999;

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Puvanendran and Brown, 2002 等），光周期（Hoover, 1937；MacQuarrie *et al*., 1978 等）や色・波長（石田ほか，1973； Downing and Litvak, 2001 等）の観点から研究がすすめられ，それらの知見に基づき，成長の促進や生残の向上に適した照明が用いられている。また，種苗生産でしばしば発生する過密飼育による形態異常，攻撃性や疾病等の問題を，光環境の制御によって解決しようとする試みも始まっている。一元的な飼育管理のもとで生じる初期減耗等の原因は，対象種にとっての最適な環境と飼育環境との相違にあると推察されている（清水ほか，2013)。屋内施設での飼育で用いられる人工光源のスペクトルは，太陽光のそれとはまったく異なっている。また水深の浅い水槽において飼育する場合が多く，水槽壁からの光の反射も加わり，飼育対象種の天然海域での光環境とは大きく異なる。

近年，LED 照明の開発・発展により，さまざまな特定波長の光を用いた飼育が可能となった。また，水銀に関する水俣条約の採択により 2021 年には蛍光灯や水銀灯は製造中止となることから，今後は一層，LED 照明への転換が進むと考えられる。LED 照明では，波長分布，配光特性や明暗周期などを自由に設定することが可能であり，魚類の生理・生態に対応した光条件の設定によりさらなる生産性の向上が期待されている。

魚類の光に関与する受容器官は眼と松果体である。眼の内側に存在する網膜には桿体と錐体の 2 種類の視細胞があり，桿体は薄明環境下で光を受容して明暗感覚に関与し，錐体は明るい環境下で色彩感覚に関与する。一方，松果体はメラトニンの分泌機能, 脳への情報伝達機能を備えている（植松ほか，2013)。

魚類の眼は，河川，海洋，濁った水，あるいは光が少ない深海等多岐にわたる生息環境の下で，餌生物の検知，捕獲，捕食者からの回避，繁殖行動等，生存していく上で重要な行動を司る受容器である。これまで魚類の視覚機能に関する研究は，対光行動を調べる行動生理学，光刺激により生じる電気信号を調べる電気生理学，網膜の組織形態学や視物質の生化学解析の各分野で分析技術が発達してきた。近年では，光を吸収するタンパク質（オプシン）の遺伝子解析を行う分子生物学の研究が盛んである。これらの研究により多くの視覚機能に関する知見が蓄積され，漁業や飼育現場で対象生物の視覚機能に適応した光環境を把握し，利用する取り組みが進んでいる。

本稿では，魚類の光受容器の知見，および光を用いた繁殖やストレス等の生理や成長，生残，初期摂餌等活動の制御に関する研究成果に焦点を絞り，人工的な光環境が及ぼす魚類の行動への影響および光を利用した種苗生産と養殖について，その効果や問題点を検討した。

2. 海域における光環境について

魚類への光の影響を検討する上で，海水中における光の特性を知る必要がある。海洋における光学的研究は Jerlov（1964）の「海洋水の光学的分類 Optical classification of oceanic waters」による成果が大きい。これは，波長別の光の透過に基づいて，外洋水（Ⅰ・IA・IB・Ⅱ・Ⅲ)，沿岸水（1, 3, 5, 7, 9）の水型に分類したものである。Jerlov（1964）はさまざまな海域の波長別の透過率から，光学的水型へあてはめた。この分類を利用すると黒潮域は外洋水ⅠB，相模湾は沿岸水 1〜3 に相当するとされる（松生，1984)。

一般的に海水中に透過した光は，海水の水分子による吸収と散乱で透過する距離に対して指数関数的に減衰する。また吸収による減衰は散乱によるものより大きく, この減衰の程度は, 波長によっても異なる（Jerlov, 1964)。海水では，波長の長い光（赤色）は海水自体によって強く吸収される。また波長の短い光（波長 450 nm ~ 500 nm; 青色や緑色）は吸収されにくい（Smith and Baker, 1981）ため，比較的深い水深まで到達する。

海水中では濁りの要因である無機・有機懸濁粒子およびそれらの分解生成物である有機溶存物質によっても光が減衰する。これら物質の濃度の増大に伴い，減衰の程度は大きくなる。この減衰は各物質による光の吸収と散乱の増大の結果である（森永，1986)。特に，有機懸濁粒子および有機溶存物質では，短波長の光の吸収が，長波長より大

きい。また，懸濁粒子の散乱は波長による違いが小さい（松生，1984）。これらのことにより，海の色は，一般に，貧栄養で低生産な熱帯では濃青色，生物生産力の大きい高緯度では緑色，また有機懸濁物質および有機溶存物質の多い富栄養の沿岸海域では黄緑色，黄色，褐色，赤色等を示す（宇田，1969）。これらの結果，魚類の生息域の環境スペクトルは，生息水深や懸濁物質等の影響を受け多様となる。

上述のように，魚類の生息場所の明るさとスペクトルは，季節，時間，水深によって変化するばかりでなく，海水に含まれる懸濁物や溶存物の濃度や種類によっても変化している。これに対して，水槽で飼育した場合，明るさとスペクトルは水深が浅く一定であることから大きく変化しない。また飼育水として濾過海水を使う場合が多く，懸濁物や溶存物による変化も限定的となる。屋内飼育の光環境は，対象種にとって海の光環境とは異なることでストレス等の影響が懸念される。一方，飼育に有効な光環境が把握できれば，選択的に光源の種類や配置によりコントロールしやすいという利点がある。

3. 魚類の色彩・明暗感覚

脊椎動物の光感覚には色を感知する色彩感覚（色覚）が含まれる。魚類の色覚に関するこれまでの研究は，末広（1960）の総説があり，以下の事例が紹介されている。古くは Bateson（1889）が色の判別実験を行うなど魚類の色覚に関する種々の実験が行われた。Hess（1909）は魚類が蝟集する光から判断して，魚類は色盲である（色覚がない）と主張した。しかし，Bauer（1910）の色ガラス等の識別実験，Von Frisch（1912）等の学習法による実験から，魚類の色覚の存在が推測されたことが紹介されている。魚類の網膜の組織観察に関する報告については田村（1977）の総説では，Von Frisch（1925）は他の脊椎動物と同様に，魚類の網膜においても環境の明るさにより暗所で働く桿体と明所で働く錐体の２つの異なる感光細胞の分業が行われているメカニズム（二元説）を有することを証明したことが記されている。桿体と錐体の視感度の違いについては，Grundfest（1932）が桿体に比べ錐体の感度は長波長にシフトしていることを推定した。Clarke（1936）は，湖や沿岸海水域の水中光スペクトル分布と魚類の視覚の高感度波長帯が類似することに着目し，深海魚の分光視感度曲線のピークが青色波長帯に見出される可能性を予測した。その後，深海魚の視物質の分光吸収特性を計測した研究（ハダカイワシ科 54 種のピーク波長 480 - 490nm（Turner *et al.*, 2009），ヒカリキンメダイ *Anomalops katoptron* 約 490 nm（Mark *et al.*, 2018）等）により実証された。川本・竹田（1950）は魚類の行動と波長の影響を明らかにする目的で, 6 魚種の稚魚（イシダイ *Oplegnathus fasciatus*，カワハギ *Monacanthus cirrhifer*，サワラ *Cybium niphonium*，クサフグ *Spheroides niphobles*，ヤマトカマス *Sphyraena japonica* 及びニホンウナギ *Anguilla japonica*）を対象に波長（白，赤，橙，黄，緑，青，藍，紫のフィルターを使用した 8 色の光源）の異なる試験区において走光性を調べた。ニホンウナギを除き大部分の魚種では青や緑の集魚率が高く, 走光性は波長の影響で生じると推測している。魚種により波長別の光応答の違いは推測されていたが，その根拠として生態の違いという観点から調べた先駆的な研究として，Kobayashi（1962）の網膜電図（ERG）の分析がある。Kobayashi（1962）は浅海域に生息するキュウセン *Halichoeres poeciloptelus* から水深 300m の深海域に生息するホシザメ *Mustelus manazo* まで海水魚 16 魚種，淡水魚 4 魚種の網膜の ERG 分析から分光視感度曲線を推定し，生息水深との関係を調べた。その結果，生息水深が深い魚種ほど分光感度ピーク波長（λ_{max}）は短波長側にシフトしており，魚の視覚機能が生息域の光環境の特性に適応したことを推測している。その後，顕微分光光度計の開発により，個々の視細胞の視物質の吸収波長を調べる研究が進展し，Loew and Lythgoe（1978）は珊瑚礁，深い沿岸，沿岸，淡水域に生息する 18 魚種について，桿体，モザイク配列を構成する錐体（単錐体，複錐体）のそれぞれ視細胞種類ごとの視物質の極大吸収波長を調べ，魚類の視物質の光環境への適

応について生態学的に考察している。

魚類の色覚が機能的に発達していることは分子生物学の分野から明らかにされている。網膜には光を受容する細胞（視細胞）があり，ここに視物質が含まれる。視物質は発色団とオプシンが結合して構成される（田村，1977）。網膜の視物質の吸収波長はオプシンの多様性により変化することから，色覚は錐体オプシンの種類数に依存すると考えられている（河村，2009）。オプシンには桿体オプシン（RH1）と錐体オプシンがあり，このうち錐体オプシンには，青－紫外線感受性（SWS1），青感受性（SWS2），緑感受性（RH2），赤－緑感受性（M/LWS）の 4 種類が存在する（Yokoyama, 2000）。魚類は桿体オプシンと錐体オプシン 4 種類とサブタイプを複数種持っている（河村，2009）。特に，ゼブラフィッシュ *Danio rerio*（Morrow *et al.*, 2011）ではサブタイプを含めて 10 種類，メダカ *Orjlzias latipes*（Matsumoto *et al.*, 2006）では 9 種類のオプシンが確認されており，霊長類のオプシン 4 種類に比べオプシンの種類が多いことが明らかになっている（河村，2009）。

視物質の発色団は，ビタミン A_1アルデヒドの 11–シス–レチナール（以下 A_1）とビタミン A_2の 11–シス 3–デヒドロレチナール（以下 A_2）の 2 種類が存在する。桿体の視物質は，A_1と桿体オプシンの組み合わせでできるロドプシン，A_2と桿体オプシンの組み合わせによるポルフィロプシンであり，ベラ科の魚を除く海産魚では一般にロドプシンを有し，淡水魚ではポルフィロプシンを有している場合が多い（植松ほか，2013）。海水と淡水を行き来する魚種では，生息域の違いでロドプシンとポルフィロプシンの比率が変わる（Beatty, 1966；Hasegawa and Miyaguchi, 1997 等）。魚類は生息域の環境に応じて，視物質の構成を変化させることが明らかになっており，通し回遊魚では海水と淡水で A_1と A_2の切り替えに加え，オプシンの発現の組み合わせを変えることがヨーロッパウナギ *Anguilla anguilla*（Archer *et al.*, 1995），ニホンウナギ（Zhang *et al.*, 2000）等で報告されている。淡水と海水では生息環境の光特性が異なるため，以上のように視物質の構成を変化させて水中の光環境へ適応させていると考えられる（河村，2009）。

魚の視感度に関する研究では，沿岸域に生息する魚類は緑や青に視感度が高い魚種の報告例が多く見られ，海水の光学的特性への適応と考えられている（Kobayashi, 1962; Lythgoe, 1979）。また通し回遊魚は，上述したようにそれぞれの生息域に対応してロドプシン等の視物質構成を変換させ，視感度を変化させるメカニズムが発達している。特定の波長に対する視感度は，魚が生息する光環境に適応する可能性が高く，これらの波長が背景に対するコントラストを高め，水中の物体を検出するのに特に有効である（Lythgoe, 1979）。このように魚類は，環境に応じて対象物に対する視認性を高めるため，オプシン遺伝子の多様性（河村，2009）があり，明度分布や吸収や散乱により波長分布が変動する水中環境に適応できるよう色覚が発達してきたと推定される（河村，2009）。

4. 魚類の行動への光の影響

飼育における光環境の影響に関する研究は，その多くが成長，生残，あるいは攻撃性に伴うストレス（血中コルチゾル濃度分析），仔魚期に特有の鰾開腔，未成魚の成熟抑制等を目的として行われてきた。本稿では，人工光が魚類に及ぼす影響について，スペクトル，光周期，明るさ（照度）の条件設定に分けて各目的に対する既往知見を Table 1，2 にまとめた。なお，本稿における光条件による影響は，多くの報告で実験項目対象となっている成長や生残，ストレス，性成熟，行動への影響を中心に取り扱うこととする。

1）スペクトル（もしくは色）

スペクトルの異なる光を照射することによる成長や行動実験は多く行われている。石田ほか（1973）は白・青・緑色の光を照射し，ヒラメ稚魚の成長を観察し，青や緑光で白光より成長が良いことを報告している。その後，色フィルターを巻いた蛍光灯や LED 照明を用いた実験が数多く行われ，成長促進や生残率向上，ストレス低減に対しては青や緑色光が有効とする報告が多い

Table 1. List of research using light : Effect of spectrum for growth (a), survival (b), stress (c), first feeding (d), reproduction (e), sex differentiation (f), and behavior (g).

Common name	Species	Reference	Recommended condiion*	Negative influence condition
Zebrafish	*Danio rerio*	VILLAMIZAR *et al*. (2014) a, b	blue (472 nm), white	Red (665 nm)
Goldfish	*Carassius auratus*	SONG *et al*. (2016) c	Green (530 nm)	Red (620 nm)
Rainbow trout	*Oncorhynchus mykiss*	HEYDARNEJAD *et al*. (2013) a, c KARAKATSOULI *et al.* (2008) a, c	Yellow (546 nm) a: Red (605 nm), c: Blue (480 nm)	
Haddock	*Melanogrammus aeglefinus*	DOWNING and LITVAK (2001) d	Blue (470 nm)	
Medaka	*Oryzias latipes*	HAYASAKA *et al.* (2019) f	Green (518 nm)	
European Sea bass	*Dicentrarchus labrax*	VILLAMIZAR *et al.* (2009) a, b	Blue (463 nm) (12 hL)	
Spotted sea bass	*Lateolabrax maculatus*	HOU *et al.* (2019) a, c	Blue (460 nm) (18 hL)	Red (625 nm)
Yellowtail clownfish	*Amphiprion clarkii*	SHIN *et al.* (2011) c, (2012) a	Blue (450 nm), green (530 nm)	Red (630 nm)
Nile tilapia	*Oreochromis niloticus*	VOLPATO and BARRETO (2001) c; VOLPATO *et al.* (2004) e ELNWISHY *et al.* (2012) a	Blue (cellophane)	
Texas cichlid	*Herichthys cyanoguttatus*	MONTAJAMI *et al.* (2012) a, b	White	
Sandfish	*Arctoscopus japonicus*	KAWAMURA *et al.* (2010) a, b in Japanese	Blue (470 nm)	
Pacific bluefin tuna	*Thunnus orientalis*	TSUTSUMI *et al.* (2014) a, b	Green (520 nm), white	Red (630 nm)
Japanese flounder	*Paralichthys olivaceus*	ISHIDA *et al.* (1973) a in Japanese	Blue, green	
Spotted halibut, Japanese flounder, slime flounder	*Verasper variegatus, Paralichthys olivaceus, Microstomus achne*	SHIMIZU (2015) a, b in Japanese	Blue (464 nm), blue-green (497 nm), green (518 nm)	Red (635 nm)
Barfin flounder	*Verasper moseri*	YAMANOME *et al*. (2009) a TAKAHASHI *et al*. (2016) a	Green (filter) Green (518 nm)	Red (filter) Red (635 nm)
Spotted halibut Japanese flounder	*Verasper variegatus, Paralichthys olivaceus*	SHIMIZU *et al.* (2019) a	Green (518 nm)	
Marbled flounder	*Pseudopleuronectes yokohamae*	UEKI *et al.* (2019) a, g; SHIBATA *et al*. (2019) c in Japanese	Green (525 nm)	Red (655 nm)
Senegal sole	*Solea senegalensis*	BLANCO-VIVES *et al.* (2010) a	Blue (435–500 nm) (12 hL)	

*When there was a plurality of light conditions, all conditions were described in one condition.
Photoperiod (light : dark;12 : 12 [12 hL])

Table 2. List of research using light: Effect of photoperiod for growth (a), survival (b), viability (b'), sexual cycle control (c), swimbladder inflation (d), first feeding (e) and aversion behavior (f). Effect of light intensity for growth (g), survival (h), swimbladder inflation (i), behavior (j) and first feeding (k).

Common name	Species	Reference	Recommended condiion	Negative influence condition
American eel	*Anguilla rostrata*	PATRICK *et al.* (1982) f	Intermittent light	
Carp	*Cyprinus carpio*	KUROKI and NAKAUMA (1953) f in Japanese	Intermittent light	
Carp, brown bullhead, largemouth bass	*Cyprinus carpio, Ameiurus nebulosus, Micropterus salmoides*	KIM and MANDRAK (2017) f	Intermittent light	
Matrinxã	*Brycon amazonicus*	MULLER *et al*. (2019) g, h, j	20 lx	
Coho salmon	*Oncorhynchus kisutch*	MACQUARRIE *et al.* (1978) c	Photoperiod change	
Atlantic salmon	*Salmo salar*	IMSLAND *et al.* (2014) a, c	24 hL	
Coho and chinook salmon	*Oncorhynchus kisutch, Oncorhynchus tshawytscha*	NEMETH and ANDERSON (1992) f	Intermittent light	
Atlantic cod	*Gadus morhua*	IMSLAND *et al.* (2007) a PUVANENDRAN and BROWN (2002) g, h	24 hL 2400 lx (24 hL)	
Haddock	*Melanogrammus aeglefinus*	DOWNING and LITVAK (1999) g DOWNING and LITVAK (2001) k	110 lx 1.8 μmol m^{-2} s^{-1}	
Pike silverside	*Chirostoma estor*	MARTÍNEZ-CHÁVEZ *et al.* (2014) a	24 hL	
European sea bas	*Dicentrarchus labrax*	CARRILLO *et al.* (1989) c (15h); BEGTASHI *et al.*	15-24 hL	
		VILLAMIZAR *et al.* (2009) a, b	12 hL (463 nm)	24 hL
Striped bass	*Morone saxatilis*	MARTIN-ROBICHAUD and PETERSON (1998) d	8 hL	
Australian bass	*Macquaria novemaculeata*	BATTAGLENE and TALBOT (1990) d	0 hL	24 hL
Barramundi	*Lates calcarifer*	FERMIN and SERONAY (1997) g, h	300 lx	
Coral trout	*Plectropomus leopardus*	YOSEDA *et al.* (2003) b, e in Japanese	24 hL	
Sevenband grouper	*Epinephelus septemfasciatus*	TERUYA *et al*. (2008) a, b, e in Japanese	24 hL	
Green sunfish	*Lepomis cyanellus*	GROSS *et al.* (1965) a	16 hL	
European perch	*Perca fluviatilis*	TAMAZOUZT *et al.* (2000) g, h	800 lx (g), 250 lx (h)	
Yellow perch	*Perca flavescens*	HINSHAW (1985) g, h	205 lx	
Greater amberjac	*Seriola dumerili*	HIRATA *et al*. (2009) a, b, d, e in Japanese	18 hL	0 hL

Yellowtail	*Seriola quinqueradiata*	TAKAHASHI (1978) f in Japanese	Intermittent light	
Japanese jack mackerel	*Trachurus japonicus*	KOIKE（1985) f in Japanese；KOIKE and MATSUIKE (1987,1988) f; KOIKE *et al.* (1991) f ; AN and ARIMOTO (1994) f in Japanese	Intermittent light	
Red sea bream	*Pagrus major*	BISWAS *et al.* (2005) a	16 hL, 24 hL	
		MATSUMOTO *et al*. (2005) f in Japanese	Intermittent light	
Striped trumpeter	*Latris lineata*	TROTTER *et al*. (2003) b'	18 hL (4 μmol m^{-2} s^{-1})	
Goldlined spinefoot	*Siganus guttatus*	DURAY and KOHNO (1988) a, b, e	24 hL	
Bigeye tuna, skipjack tuna	*Thunnus obesus, Katsuwonus pelamis*	OSHIMA *et al.* (2019) f	Intermittent light	
Atlantic halibut	*Hippoglossus hippoglossus*	SIMENSEN *et al.* (2000) a	24 hL	
Greenback flounder	*Rhombosolea tapirina*	HART *et al.* (1996) a, b	18-24 hL (a)	0 hL (b)
Senegal sole	*Solea senegalensis*	BLANCO-VIVES *et al.* (2010) a	12 hL (blue)	0 hL, 24 hL
Tiger puffer	*Takifugu rubripes*	HATANAKA *et al.* (1997) g, j in Japanese	1000 lx	
Obscure puffer	*Takifugu obscurus*	SHI *et al.* (2010) a, b	24 hL	

*When there was a plurality of light conditions, all conditions were described in one condition.
*Photoperiod (light : dark; 24 : 0 [24 hL], 18 : 6 [18 hL], 12 : 12 [12 hL], 0 : 24 [0 hL])

（Table 1）。また，青や緑光は仔魚の摂食開始（DOWNING and LITVAK, 2001），性転換（HAYASAKA *et al*., 2019）にも影響を与えることが報告されている。

成長促進に効果が見られたスペクトルの光は，生残率も高い効果が得られる傾向がある（VILLAMIZAR *et al*., 2009；清水ほか，2013 等）。特に仔魚は摂餌が初期減耗に大きく影響するので，光の照射で摂餌の成功に効果があれば，生残率向上とともに成長促進にも反映される。光の波長が成長を促進するメカニズムについて，マツカワ *Verasper moseri*（TAKAHASHI *et al*., 2016），ホシガレイ *Verasper variegatus*,（SHIMIZU *et al*., 2019）で，緑（518 nm）の照明がメラニン凝集ホルモン（MCH）等に作用し，結果的に成長促進すると推定されている。

一方，淡水魚では青や緑以外で成長促進効果が得られている。通し回遊魚であるニジマス *Oncorhynchus mykiss* では，黄（主波長; 546 nm, HEYDARNEJAD *et al*., 2013）および赤（605 nm, KARAKATSOULI *et al*., 2008）で成長促進が期待されることが報告されている。同じ魚種であっても有効な波長が異なる結果となったことについては，供試魚の平均体重が 32.27g（HEYDARNEJAD *et al*., 2013）および 145.3g（KARAKATSOULI *et al*., 2008）と異なることから，成長に伴う視感度の変化による可能性が考えられる。

魚類は成長に伴って生息域が変化することが知られており，海産魚の場合，仔魚から稚魚，成魚と成長するに従い，生息水深が深くなる場合が多い。通し回遊魚の場合，例えばサケ科であれば川で稚魚期を過ごし，成長するとスモルト（銀毛）となって降海する。このように成長による生息域の変化に伴い，光環境が変化し，それに対応して

視覚特性が変化することが推定される。成長による視覚特性の変化については電気生理学手法による black bream *Acanthopagrus butcheri*（SHAND *et al*., 2002）やマコガレイ *Pseudopleuronectes yokohamae*（柴田ほか，2019），分子生物学的手法によるマツカワ（KASAGI *et al*., 2015）やクエ *Epinephelus bruneus*（MATSUMOTO and ISHIBASHI, 2016）等の報告があり，成長段階で視感度やオプシンの発現量が異なることが報告されている。

次にストレスやそれに伴う行動への影響について述べる。植木ほか（2019）は，マコガレイ稚魚を対象に，対照区（水銀灯＋蛍光灯），赤（655 nm），青（465 nm），緑（525 nm）の LED 照明下で 50 日間飼育し嚙み合いによる尾鰭欠損を生じた異形魚の出現率と成長を比較した。その結果，緑 LED が噛み合い行動を抑制し，成長に効果があることを報告している。また，マコガレイ稚魚の血中コルチゾル濃度は，緑や青の照明で低減し，ストレスを低下させる可能性が示唆された（SHIBATA *et al*., 2019）。ストレスに対する色（波長）の効果は，海水魚や淡水魚に共通して，青や緑に正の効果があるとする報告が多い（Table 1）。キンギョ *Carassius auratus* を用いて白色蛍光灯（対照区），緑（530 nm）および赤（620 nm）の LED 照明を 4 週間照射した実験（SONG *et al*., 2016）では，光による網膜のダメージとストレスを波長別に評価している。当該実験では，網膜のダメージとストレスの指標としてコルチゾル濃度，過酸化水素（H_2O_2）濃度，カスパーゼ-3 活性および濃度を比較した。その結果，緑は他の光照射よりすべての指標物質濃度で低下が見られたが，赤では逆に増加が示された。また，赤照明による網膜のダメージは，アポトーシス（細胞の死）を誘発する可能性があることを推定している。

上記で示したように魚類の飼育に青や緑波長の光を使用すると，成長促進や生残率向上，そしてストレス低下などの効果が複合的にみられる。魚類の生息環境において光の波長分布をいかに選択するかは効率的な飼育を行う上で極めて重要であり，今後も行動や生理分野も含めて魚種毎の光に対する生理，生態への応答の分析が必要である。

2）光周期

魚類への光の影響としては，波長の差違によるものだけではなく，季節毎の日照時間の変化も挙げられる。自然環境下における魚類の生理機能や行動は，水温や日照時間といった環境要因の影響を複合的に受け，遊泳リズム，摂餌リズムや生殖リズムなどの生体リズムが誘導される（鈴木ほか，2013）。

光周期の変化によって動物の性周期を変化させる（例えば，非繁殖期に生殖腺の発達や繁殖行動を誘導させる）という研究の試みは，1920 年代に鳥類から始まり，ほ乳類まで広がった（HOOVER and HUBBARD, 1937）。魚類についての研究では，カワマス *Salvelinus fontinalis* に対して，日長サイクルの変化による産卵の誘発（HOOVER, 1937；HOOVER and HUBBARD，1937），および誘発と遅延（HAZARD and EDDY，1951）が報告されている。毎日産卵する魚種では特定の時刻に産卵する生殖日周期が存在する。シロギス *Sillago japonica* の産卵時間は，明暗周期の変化によって，明期の開始時刻が産卵リズムに影響を与えることが報告されている（古川ほか，1991）。光周期を変化させて性周期を操作する実験では，産卵期以外での成熟や，未成魚の成熟抑制の報告がある（Table 2）。また，成長や組織の発達，生残等の比較実験が行われ，仔魚期では，鰾の開腔（開鰾）に関してさまざまな魚種で報告がある（Table 2）。開鰾の促進には短日あるいは暗闇で効果がある事例が多い（Table 2）。逆に，生残率向上や成長促進の試験では，18 時間や 24 時間の長日照明で効果が得られるとの報告事例が多い（Table 2）。

開鰾に短日照明あるいは暗闇の条件により効果がある要因として，BATTAGLENE *et al*.（1994）はキス科の sand whiting *Sillago ciliata* 仔魚は夜間に浮上し，開鰾を開始する日周性があることを観察した。TROTTER *et al*.（2003）は，暗闇の始まりが開鰾のきっかけとなる可能性を示唆している。一方，長日照明により成長促進効果が得られる要因は，摂餌の機会が拡大することや松果体による内分泌への影響が考えられる。しかし，光周期を変化させても成長等にあまり影響を与えないとする

報告もある（HALLARÅKER *et al.*, 1995; PURCHASE *et al.*, 2000; DOWNING and LITVAK, 2000）。Turbot *Scophthalmus maximus*（IMSLAND *et al.*, 1995）や Atlantic halibut *Hippoglossus hippoglossus*（JONASSEN *et al.*, 2000）の報告では，光周期による成長促進の効果は水温の影響を受ける可能性があることが示されている。光の効果を調べる実験設定には，水温などの他の条件も注視することが必要であろう。

上記の光周期による試験は，連続的な長周期（周期；時間）による試験であるが，断続光（周期；秒）に対する魚の忌避行動を利用して，湾内における魚群行動制御や漁網に対する行動の制御を目的とした行動実験も，さまざまな魚類に対して行われている（Table 2）。マアジ *Trachurus japonicus* を用いた断続光に対する行動実験では，明暗の周期や照度，色に対する忌避効果の評価が行われている（小池，1985；KOIKE and MATSUIKE, 1987,1988; 小池ほか，1991）。またメバチ *Thunnus obesus* 若齢魚の混獲防除のため，断続光により流れ物付き（FADs）操業時の漁網への回避行動の可能性も示されており（OSHIMA *et al.*, 2019），断続光による行動制御の資源管理への応用が期待される。

連続光の長周期の設定は魚類にとって初期段階から生残や成長に大きく影響する。他方，断続光は忌避効果が期待され，回避させたい海域への侵入阻止の可能性がある。連続光と断続光に対する魚の応答は相反するが，行動制御として有効な技術であり，今後も多くの魚種で検討されることを期待したい。

3）明るさ（照度）

光周期とともに光の明るさ（照度）も魚類の視覚への影響が大きい。光の感受性は網膜構造の違いから生じる。ほとんどの仔魚は単錐体のみを有し，変態後に桿体を発達させる（BLAXTER and STAIN, 1970）ことから，照度の感受性が成長段階で変化する可能性がある（PUVANENDRAN and BROWN, 2002）。仔魚にとって，内部栄養から外部栄養へと切り替わる初回摂餌の期間は，その後の生残を決定づける重要な時期とされる（BLAXTER and HEMPEL, 1963; KOHNO, 1998）。仔魚の開口時に餌の確認を可能とする最適な光条件を与えることは，生残率向上のための必須条件と考えられる。多くの魚種は約 0.1 lx で摂食が可能となる照度閾値を有している（BLAXTER, 1986）。しかし，仔魚は桿体がなく光受容器官が未発達であるため，照度が高い方が成長や生残に対する効果が得られる事例は多い（Table 2）。実験で使用される照度のレベルは様々だが，たとえば haddock *Melanogrammus aeglefinus* では 5 lx と 110 lx では 110 lx の方が成長・生残は良い結果が得られている（DOWNING and LITVAK, 1999）。また striped trumpeter *Latris lineata* 仔魚は 4 μmol m^{-2} s^{-1} と 40 μmol m^{-2} s^{-1} の照明条件の比較で 4 μmol m^{-2} s^{-1} で開鰾後の生存率が高いこと（TROTTER *et al.*, 2003），Atlantic cod *Gadus morhua* は 300，600，1200，2400 lx の照度では 2400 lx で最も成長・生残率が良いことが報告されている（PUVANENDRAN and BROWN, 2002）。

光の感受性の差異は成長段階だけではなく，魚種毎で異なる場合がある。同じ異体類でもヒラメ *Paralichthys olivaceus*，ホシガレイ，ババガレイ *Microstomus achne* の仔魚を対象に光量子量（0～22.8 μmol m^{-2} s^{-1} の 5 段階）を変えて白色蛍光灯で飼育したところ，成長や生残に良好な光量子量はホシガレイ＞ヒラメ＞ババガレイの順であり，生息水深が浅い魚種ほど成長や生残に適した光量子量が高いこと，摂餌可能な光量子量は成長に伴い低下していくことが報告されている（清水ほか，2013）。カタクチイワシ *Engraulis japonicus* の網膜には，深海魚に多いタペータム（tapetum）という弱い光を反射させる光反射板が存在し薄明環境に適している（AWAIWANONT *et al.*, 2001）。このことはカタクチイワシがタペータムを有しない他の沿岸魚と光の感受性が異なる可能性を示唆している。その例として次のような報告がある。藤井ほか（2016）はカタクチイワシの視覚機能と特定波長照明による対光行動の試験を行った。この結果，カタクチイワシの仔魚では青緑から緑，成魚では紫から緑にかけて感度が高いことを明らかに

した。一方，青と赤色 LED 照明による行動実験では，仔魚は青色の光に蝟集したが，成魚は赤色の光に蝟集し，感度が高い青の光では照明から離れた場所で遊泳したことが示された。すなわち，仔魚は感度の高い波長の光に蝟集し，成魚では高感度の波長の光を回避する正反対の行動が示されたわけである。成魚の赤い光への蝟集行動は，カタクチイワシの網膜に存在するタペータムの影響や光に対する嗜好性等の要因の可能性があると示唆されるが，内分泌の影響も含めて今後もメカニズムの解明が待たれる。このように，成長段階や魚種によって光の感受性の違いが推測される。スペクトルや周期とともに照度条件も行動制御を行う上で重要であるといえる。

4）光の悪影響

光は魚類の行動制御に有効であるが，魚種によっては制御方法を誤ると飼育に悪影響を及ぼすことがある。たとえば仔魚の開鰾には暗条件が適している魚種が多いが，カンパチ *Seriola dumerili* 仔魚は暗条件では開鰾がほとんど観察されない（平田ほか，2009）。European sea bass *Dicentrachus labrax* の仔魚では 17 日間の 24 時間連続照明によって顎の伸長や鰾肥大の奇形および開鰾未発達等が観察された（Villamizar *et al.*, 2009）。ホシガレイ仔魚では連続照明で成長促進が示されたものの，2 週間以上の長期間にわたり照明を継続すると，白化個体が増加することが報告されている（清水，2015）。Senegal sole *Solea senegalensis* は連続照明あるいは暗闇で，変態前（17 日）までに死亡している（Blanco-Vives *et al.*, 2010）。長日照明は成長促進等に効果がある事例が多い一方で，過度な照射時間により上記のように奇形や色素異常等の弊害をもたらすことがある。また，波長の違いによる飼育実験で赤が他の色に比べ成長が劣る事例が仔魚や稚魚を対象に多数報告されている（Table 1）。その要因として，多くの仔魚には，赤の波長に λ_{max} を示す錐体視物質がない（Britt *et al.*, 2001）ため，餌の視認能力の低下，内分泌の影響による摂餌不良（Takahashi *et al.*, 2016）等が考えられる。

上述のように，光条件は仔魚期では生残率に大きく影響を及ぼす。光条件を検討する際は，発達段階，優先する目的，飼育環境や期間等を総合的に考慮する必要がある。

5. 結論

組織学，分子生物学，電気生理学，行動学等の多方面にわたる多くの既往知見から，生息する環境の光条件の中で魚類の視覚機能がいかに強化され，それが生理・生態に反映されてきたかが明らかにされた。一方，一般的な生息環境中に存在しない 24 時間照明や断続光の利用でも，行動制御の効果を示す報告は多い。

このように視覚機能に対応し，適切な光の条件を選択することにより，多くの魚種において，行動制御の可能性がある。対象となる魚種の視覚特性を解明し，その生態を考慮しつつ照明技術として応用することは，対象種が有している視覚能力をより向上させる可能性が高いが，先述したカタクチイワシの例のように，視感度と行動が必ずしも一致しない例が存在する。

以上から，漁業や種苗生産，養殖業に効果的な光条件を把握するためには，仔魚から成魚までのすべてのステージでの生態を把握し，ステージごとに変化する視覚特性，対光行動，生理現象を総合的に理解することが必要である。

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Effect of wind on seawater exchange in Matsushima Bay

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Abstract: To examine seawater exchange in Matsushima Bay, we analyzed monthly temperature and salinity data, obtained by the Miyagi Prefecture, and temperature monitoring data provided by the Sena and Varns Corporation. The difference in surface temperature, between water inside and outside of the bay, is larger in early summer and late summer, and decreases in mid summer, indicating two peaks in the warming season. A temperature fluctuation with a several-day period was strongly correlated to the northwest-southeast wind component, which dominated from early summer to fall. The correlation indicates that the temperature decrease was induced about 2 days after southeastward wind events. In order to clarify these mechanisms, we employed the Regional Ocean Modeling system (ROMS) using observed atmospheric data. After reproducing the temperature variation from spring to fall, we found that over a several-day period, wind induced seawater exchange and variation in the temperature difference between water inside and outside of Matsushima Bay. Monitoring data and model results confirmed that an internal tide was generated in the bay during the formation of a thermocline that occurred after the southeastward wind. These results indicate that wind-induced seawater exchange occurs in Matsushima Bay.

Keywords : *seawater exchange, wind effect, internal wave, ROMS*

1. Introduction

Matsushima Bay is located in the northwest of Sendai Bay, Japan, which is connected to the Pacific Ocean (Fig. 1). The width of the mouth of Matsushima Bay (w) is about 1.7 km, and the area (s) is approximately 35.3 km^2. The maximum depth in the bay mouth (d_1) and the water depth inside Matsushima Bay (d_2) are both approximately 4 m (average depth = about 3 m). According to the formula for the geographical enclosed index ($r = d_2\sqrt{s} / d_1 w$; WADA, 1989), the index for Matsushima Bay is approximately 3.5. From the table of geographical enclosed indices (INTERNATIONAL EMECS CENTER, 2001), the indices for Tokyo Bay and Osaka Bay are 4.2 and 3.4, respectively. Since a geographical enclosed index greater than 2 indicates that a bay is enclosed (WADA, 1989), Matsushima Bay is categorized as an enclosed bay, like Osaka Bay.

Matsushima Bay is a famous oyster-cultivation area, but high oyster mortality has been reported in recent times. An exceptionally low oyster seedling yield was recorded in 2013, despite a higher density of early-stage larvae than

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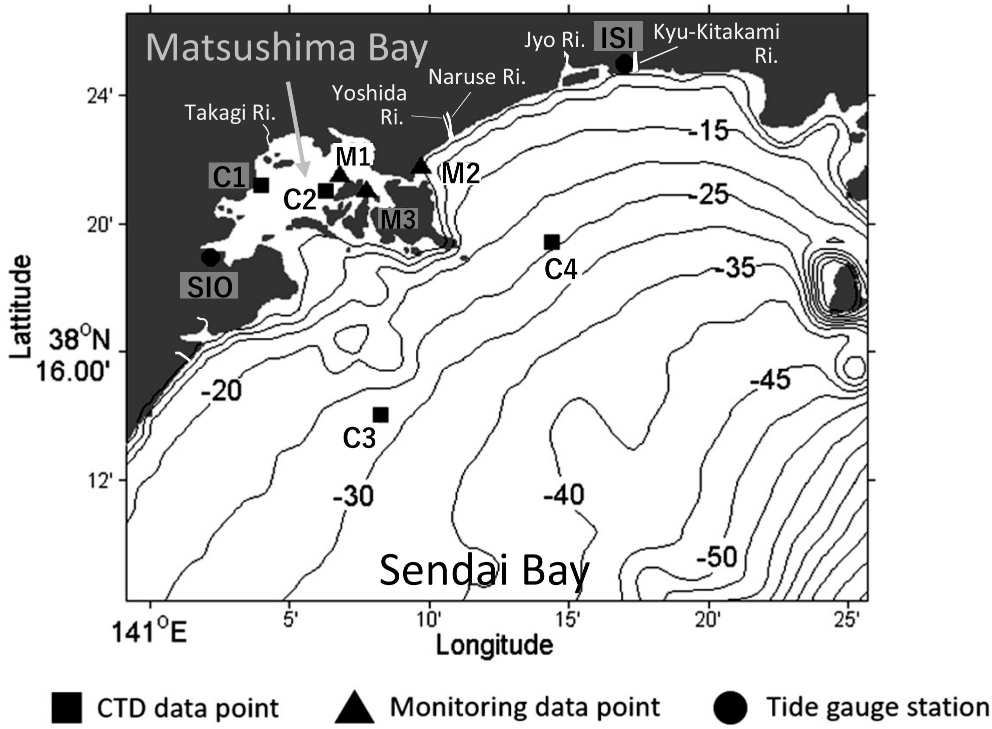

Fig. 1 Locations of monthly CTD observation stations (C1 to C4), monitoring stations (M1 to M3), and tide-gauge stations (SIO and ISI) in the northwest of Sendai Bay.

in previous years. KAKEHI et al. (2017) reported that the unusually low surface salinity in August 2013 enhanced estuary circulation, and early-stage oyster larvae were transported out of the bay before they reached the pre-attachment stage. Thus, the oyster seedling yield is thought to be closely related to seawater exchange in northwestern Sendai Bay. To understand the advection and diffusion of seedlings, it is necessary to clarify the mechanism of seawater exchange.

Previous studies have indicated that estuary circulation and tidal current are important processes for seawater exchange in Matsushima Bay. SHIRAI et al. (2019) conducted a high-resolution numerical experiment on Matsushima Bay and clarified the process of low-salinity water flowing into the surface waters of the bay. The effect of wind, as an external force, was included in the numerical simulation conducted by Shirai et al. (2019), but the effect of wind on circulation and water exchange was not explicitly discussed. Although numerical experiments have been conducted, the mechanisms of seawater exchange between Matsushima Bay and Sendai Bay remain an unsolved issue. Wind-driven circulation sometimes dominates in enclosed bays, such as in Tokyo Bay in the weak river-discharge season (NAGASHIMA and OKAZAKI, 1979; GUO and YANAGI, 1995; 1996). Wind forcing can act as a direct driving force of current and circulation in Matsushima Bay, while the rotation effect is not essential to circulation in such a small bay. In this study, we examine the characteristics of water condition and wind variation related to water exchange, and then attempt to explain them using a numerical model.

2. Observational data

To examine oceanic conditions within Matsushima Bay and Sendai Bay, we analyzed a dataset of temperature, salinity, and dissolved oxygen (DO) measurements, recorded in this area from 2014 to 2017, along with sea level data and meteorological data (Fig. 1). The Matsushima Bay data were obtained by Conductivity Temperature and Depth profiler (CTD) by the Miyagi Prefectural Government once every two months, while the Sendai Bay data were obtained once a month. Sea level data were collected at the Shiogama (SIO, Fig. 1) and Ishinomaki (ISI, Fig. 1) stations by the Japan Meteorological Agency (JMA). Precipitation data were collected at the Shiogama and Ishinomaki stations through the Automated Meteorological Data Acquisition System (AMEDAS) maintained by the JMA. In this area, a monitoring buoy system constructed by the Sena and Vans Corporation observed sea surface temperature (SST) once every hour from April 2nd, 2016 to March 30th, 2017 at three locations (Fig. 1). This SST dataset was used to examine inter-seasonal variation with high temporal resolution.

3. Characteristics of observational data

3.1 Temporal variability of seawater properties

The time series of temperature, salinity, and DO recorded at C1 at the surface and bottom of Matsushima Bay (Fig. 2a), clearly show seasonal temperature variability, with the lowest temperatures recorded in February and the highest recorded in August. The temporal variability of salinity and DO are similar but show opposite variation to that of temperature, i. e. low in summer and high in winter. All water properties indicate a homogeneous water structure at C1. Figure 2b shows the time series of the same properties observed at C3 at depths of 0 m (surface), 10 m, and 20 m. The difference in temperature between 0 m and 10 m, or 20 m, shows that temperature stratification was strongly developed between April and September, but became disrupted from October. The highest temperature occurred in August every year. Salinity at the sea surface was lower than at other depths, and a decrease in salinity occurred in July. However, abnormally low salinities were recorded at the surface in 2016 and 2017. The AMEDAS data indicate this was related to rainfall that occurred before the observation date (not shown). At a depth of 20 m, the lowest DO occurred in September, while the lowest DO at 0 m and 10 m was recorded in August. The measurements indicate that there is little difference between the surface and bottom layers in terms of DO. Although Matsushima Bay is geographically classified as a closed bay, the almost-uniform vertical distribution of DO during the summer stratification period suggests there was enhanced vertical mixing.

There is a slight difference in temperature between the waters of Matsushima Bay (Fig. 2c, upper panel) and those obtained from the rest of Sendai Bay. The temperature difference between C3 and C1 was therefore investigated (Fig. 2c, lower panel). The temperature difference showed two peaks during the warming period (from April to August). This is an interesting feature because during the warming period, the temperature within the bay is expected to be generally higher than that outside the bay. If both areas receive the same amount of heat, the inner bay, with a smaller heat capacity, will heat up more than the open sea. The heat capacity of Matsushima Bay, which is semi-enclosed and shallow, is smaller than that of Sendai Bay, but shows two peaks every year, implying that something induced relative heat loss in Matsushima Bay, or relative heat gain in Sendai Bay.

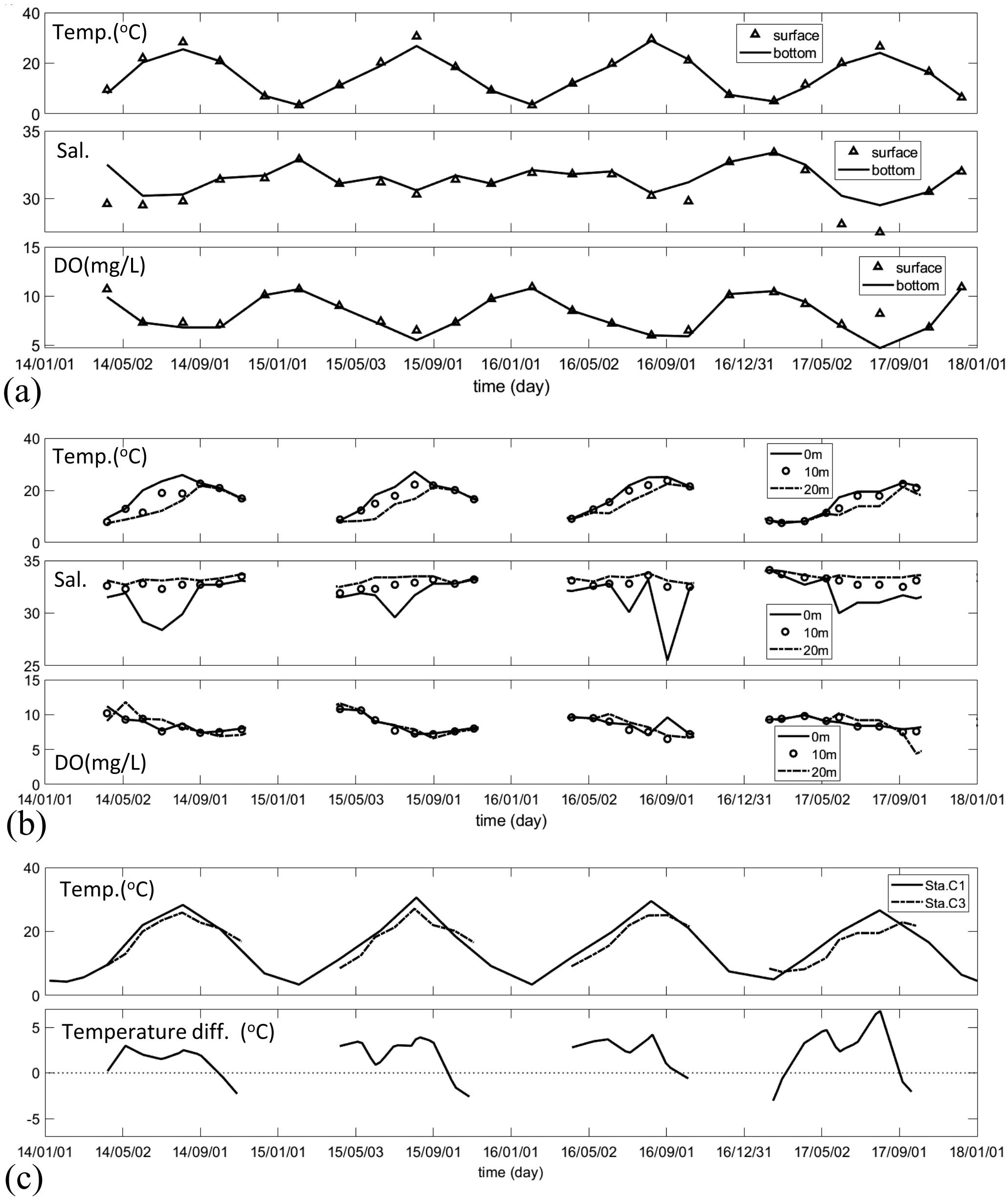

Fig. 2 Time series of temperature, salinity, and dissolved oxygen observed by the Miyagi Prefectural Government at (a) C1 and (b) C3 in Matsushima Bay. (c) Time series of surface temperature at C1 and C3, and temperature difference between C1 and C3. Two peaks in temperature difference are notable in the warming season every year.

Based on the spatial scale of the study area, the two peaks of temperature difference (Fig. 2c, lower panel) are difficult to attribute to heat flux from the atmosphere. Hence, it may be related to the differences in seawater exchange between these two areas. Thus, we tried to approach the

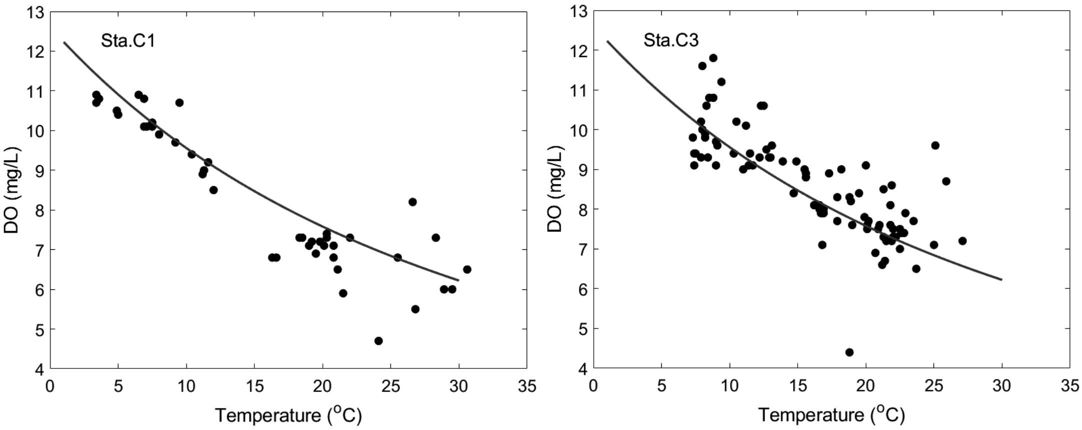

Fig. 3 Relationship between seawater temperature and DO, at inside (Sta. C1) and outside (Sta. C3) of Matsushima Bay. The black curve is the dissolved oxygen saturation curve.

mechanism of seawater exchange by understanding this twin-peak mechanism.

Because DO fluctuates seasonally and is low in summer, it is important to confirm whether low-DO water is also formed in the bottom layer of Matsushima Bay. This would indicate the strengthening of summer stratification, which is often observed in other enclosed sea areas such as Tokyo Bay. Figure 3 shows the relationship between temperature and DO at C1 and C3. The black curve is the dissolved oxygen saturation curve, which is calculated using the dissolved-oxygen formula (WEISS, 1970). The observation data were distributed around the curve, indicating that DO was saturated during the study period. That is, although DO is low in summer, the water mass of Matsushima Bay is not extremely deoxygenated, even during summer stratification, suggesting that there is moderate mixing between inner bay seawater and river water or seawater outside the bay.

We compared the daily mean water temperatures from March 2016 to November 2016, obtained at M1 and M2 using a monitoring system, with those recorded at C2 and C4 (CTD data) (Fig. 4). The water temperatures at M1 and M2 are generally similar to those at C2 and C4. Features of the CTD data are also evident, such as the rise in temperature towards August, and higher temperatures inside the bay than outside the bay. Although monitoring was conducted near the shore, the water temperature observed by the monitoring system suggested to be representative of the broader sea area. The continuous water temperature monitoring data shows remarkable several-day fluctuations in addition to seasonal fluctuations.

3.2 Wind data characteristics

The relationship between several-day temperature fluctuations and the local wind conditions was examined because the several-day fluctuations (Fig. 4) were thought to be related to the wind along the east coast of Honshu (KITADE et al., 1998; KITADE and MATSUYAMA, 2000). Figure 5a shows that the predominant wind direction was from the northwest, between October and December. From April to September, the winds in the northwest of Sendai Bay showed more variation, with the wind rose diagram (Fig. 5b) indicating that the wind was mainly from the northwest and the southeast, approximately 23%

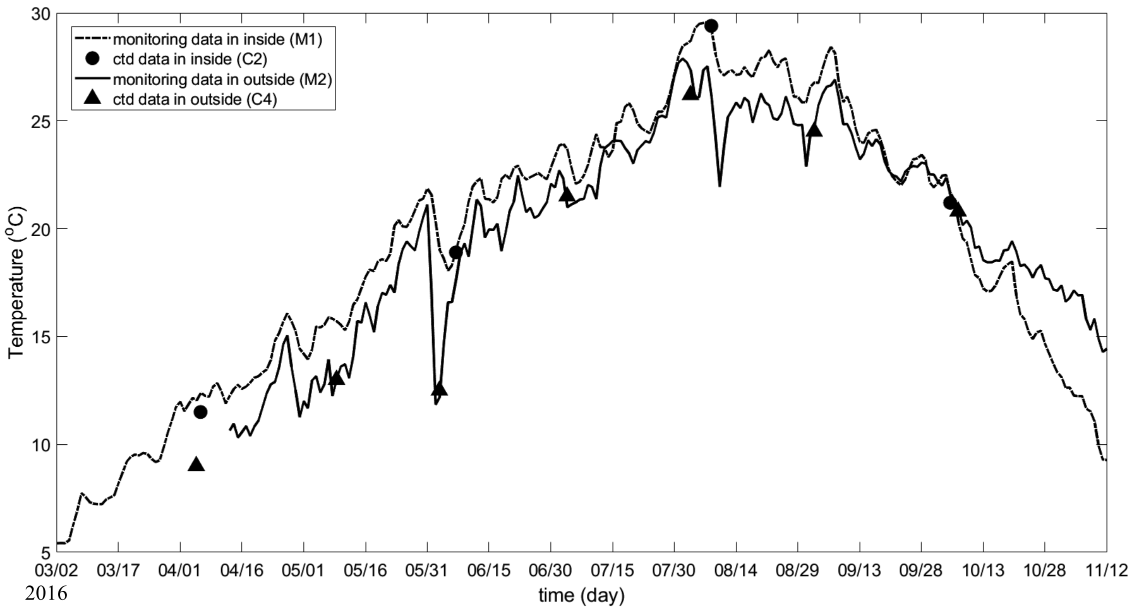

Fig. 4 Time series of daily average temperature obtained by the monitoring system at M1 and M2. The surface temperature observed by the Miyagi Prefecture Government is also indicated by the symbols ● and ▲.

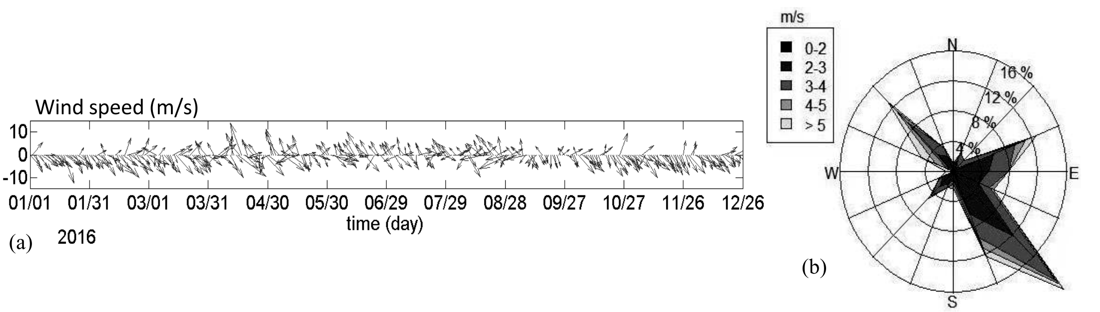

Fig. 5 (a) Time series of wind vectors. (b) Wind rose diagram from April to September 2016.

and 13%, respectively. The cross-correlation between the northwest-southeast component of the wind and the water temperature fluctuations was examined using a band-pass filter data from 25 hours to 10 days (Fig. 6). In all months except June, the absolute value of the correlation coefficient is highest in the negative time lag region, when the water temperature fluctuation occurs after there has been significant wind blowing. The negative correlation coefficient implies that an SST minimum was typically induced between 24 h and 75 h after the northwest wind maximum (Table 1). The correlation coefficient and time lag fluctuate from month to month, but this is expected, as the water temperature distribution and stratification, within the bay and beyond it, are not always the same. These results suggest that the seawater exchange and stratification in Matsushima Bay is related to the northwest-southeast component of the wind.

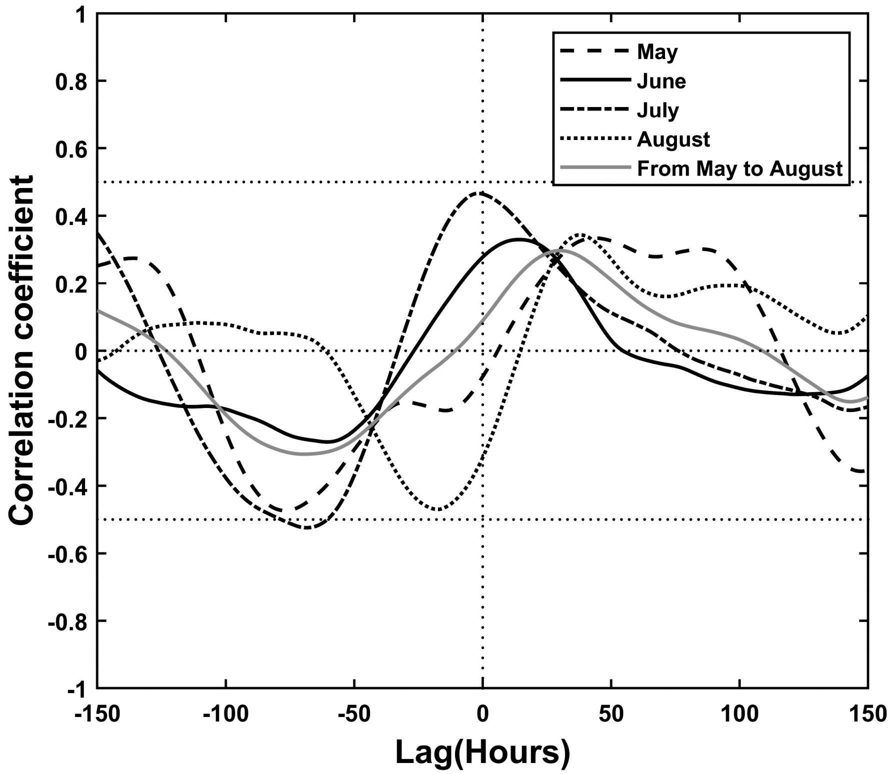

Fig. 6 Lag correlation between northwest-southeast component of wind and temperature fluctuation. A band-pass filter of 25 h - 10 days was applied to both wind and temperature data. A negative time lag indicates that the temperature fluctuation occurs after the wind has been blowing.

Table 1. Lag correlation between northwest-southeast wind component and temperature fluctuations over several-day periods.

	May	Jun	July	August	May-Aug.
Correlation coeff.	−0.45	−0.3	−0.5	−0.45	−0.4
Time Lag (hour)	75	50	60	24	60

3.3 Summary and discussion of the observational results

In the northwest of Sendai Bay, the temperature stratification gradually increased during the warming season, as shown in Fig. 2. Since the specific heat capacity of Matsushima Bay is much less than that of the rest of Sendai Bay, Matsushima Bay experienced a more significant temperature increase during the warming season. A decrease in DO during the warming season was related to a decrease in saturated oxygen due to the increase in temperature. According to CTD data, the difference in sea surface temperatures, between water inside and outside of Matsushima Bay, shows two peaks in the warming season. Continuous monitoring data indicated that the water temperature fluctuated over a period of several days, and that the fluctuation was well correlated with the northwest-southeast wind component. This suggests that the wind causes inflow and outflow of seawater through the Matsushima Bay mouth, resulting in seawater exchange and limiting stratification of the bay.

However, some unexplained aspects of this phenomenon remain, including: 1) how the unsteady winds, that blow from different directions between April and September, affect seawater transport and temperature; 2) the mechanism responsible for the two peaks in the temperature difference between water inside and outside of Matsushima Bay; 3) the relationship between tide and seawater exchange in the northwest of Sendai Bay. Because the observation data are insufficient to clarify these unknowns, we will use a numerical model to answer these questions.

4. Modeling and reconstruction

4.1 Model and conditions

The Regional Ocean Modeling system (ROMS) used in our experiment is a three-dimensional nonlinear primitive equation model, which is a modified and improved version of the SCRUM (the *S*-coordinate Rutgers University Model) developed by Rutgers University and University of California, Los Angeles. The model state variables were staggered using an Arakawa C-grid. ROMS uses an *s*-coordination system for vertical discretization, which considers the surface change in the σ-coordination system. The ROMS governing equations are discretized over variable topography using a stretched, terrain-following, vertical coordinate.

The model area covers the northwest region of Sendai Bay (latitude: 38.0423° N - 38.5089° N, longitude: 140.9263° E - 141.5346° E, Fig. 7a). The coastline is drawn from the data of the Global

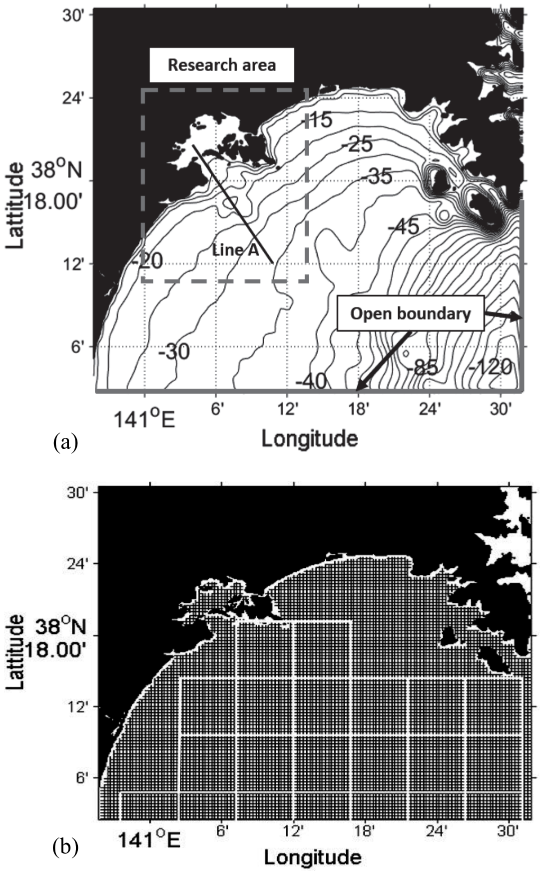

Fig. 7 (a) The model area and main research area (dashed gray line), and the south and north boundaries (solid gray line) that were set as open boundaries. (b) Distribution of the horizontal grid. The black and white grids are from ROMS and HYCOM, respectively.

Self-consistent, Hierarchical, High-resolution Shoreline Database (GSHHS). The bathymetry dataset used in this study is JTOPO30, distributed by the Marine Information Research Center of the Japan Hydrographic Association (http://www.mirc.jha.jp/products/JTOPO30v2/). The dataset has a horizontal resolution of 0.0041° × 0.0041° (black grid in Fig. 7b), and the vertical direction was divided into ten layers. The model represents the period from January 1^{st} to De-

Table 2. Boundary conditions applied in the model.

	Open boundary	Coastal boundary
Surface elevation	Chapman B.C.	Close
2-D velocity	Flather B.C.	Close
3-D velocity	Clamped B.C.	Close
Energy scattered	Gradient B.C.	Close

cember 31st, 2016 as continuous monitoring data is limited to 2016. The initial conditions and boundary conditions for temperature and salinity were provided by the World Ocean Atlas 2009 (WOA2009, global grid 1° × 1°, monthly) and by HYCOM + NCODA Global Reanalysis (resolution: 1/12°, latitude: 37.04°N - 39.04°N, longitude: 140°E - 142.96°E), respectively. The high-resolution ROMS required approximately 7 days of spin-up time at the boundary areas. The boundary conditions for two-dimensional or three-dimensional velocity, surface elevation and scattered energy were as per the conditions of FLATHER (1976) and CHAPMAN (1985), and are presented in Table 2.

The sea surface heat and freshwater flux conditions were determined from daily reanalysis data of the National Centers for Environmental Prediction (NCEP-DOE AMIP-II reanalysis-2, global grids at varying resolutions), and daily precipitation data obtained by the JMA. These datasets were temporally interpolated and applied homogeneously in our model area at every time step. The daily wind data obtained by the JMA were also temporally interpolated and were applied homogeneously as sea surface wind stress conditions.

Eight constituent tides (M2, S2, N2, K2, K1, O1, P1, and Q1) were added on the open boundary from the TPXO7 dataset (http://volkov.oce.orst.edu/tides/TPXO7.2.html) to drive the seawater movement. The correlation coefficients (R) between observations and model results, for sea level fluctuation at Ishinomaki and Shiogama, were 0.95 and 0.96, respectively. Variation in surface tide was well reproduced by this model.

Simulated results and comparison with observational data

In this subsection, we examine the reproducibility of the model by comparing water temperature and salinity fluctuations, and fluctuations in SST differences within Matsushima bay and beyond it.

First, the seasonal variations in water temperature and salinity at the CTD stations were compared with the model results (Fig. 8). While water temperature and salinity are almost vertically uniform in Matsushima Bay due to its shallow depth (Fig. 8a), stratification formed outside the bay from April (Fig. 8b). The model exhibits similar vertical differences in both temperature and salinity to those observed by the CTD stations (Fig. 8b). Therefore, the seasonal changes in water temperature and salinity observed by CTD have been reasonably reproduced by the model.

The model-calculated temperature difference, between Matsushima Bay and the rest of Sendai Bay, was compared with the temperature differences from the CTD data, as was the northwestern wind component. The fluctuation in temperature difference (Fig. 9a) seems to correspond to the three-day moving averaged wind (Fig. 8b, black line). When the wind is from the southeast (negative value of wind), the temperature differ-

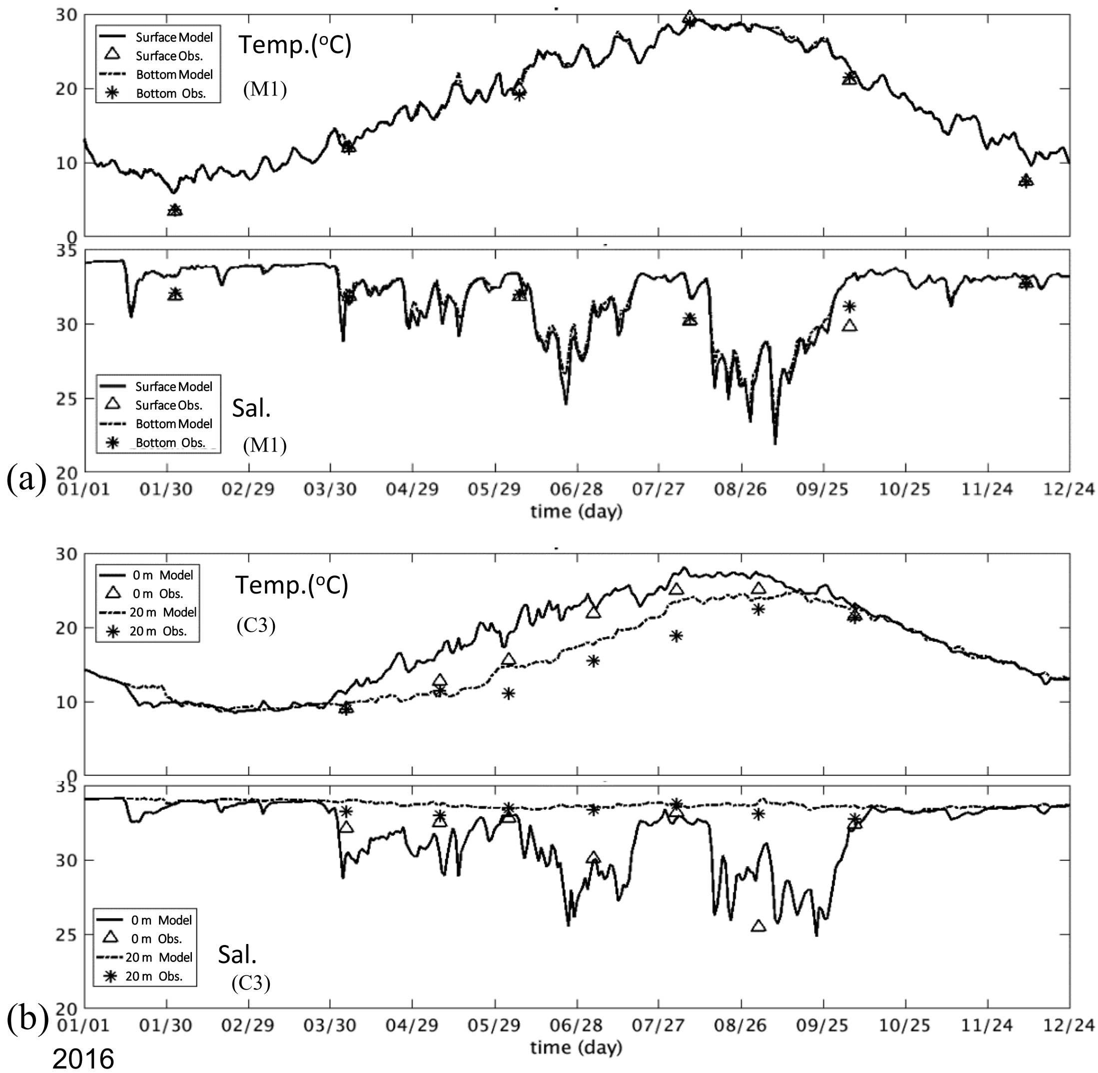

Fig. 8 Comparison between model results and observations from (a) Matsushima Bay and (b) the rest of Sendai Bay. Surface values calculated by the model are indicated by solid and dotted lines. The surface values obtained by the CTD observation are indicated by a triangle and an asterisk.

ence tends to increase. On the contrary, when the wind is from the northwest (positive value), the temperature difference tends to decrease. Although the absolute value of the water temperature is higher in the observed CTD data than in the model, the seasonal variation characteristics are reproduced without contradiction. For example, the temperature difference is larger in periods I and III than in period II, in both the CTD data and the model. Periods I and III correspond to wind from the southeast, while period II corresponds to wind from the northwest. In other words, the temperature difference is large when the wind blows from the southeast, towards the bay, and small when the wind blows from the northwest, away from the bay.

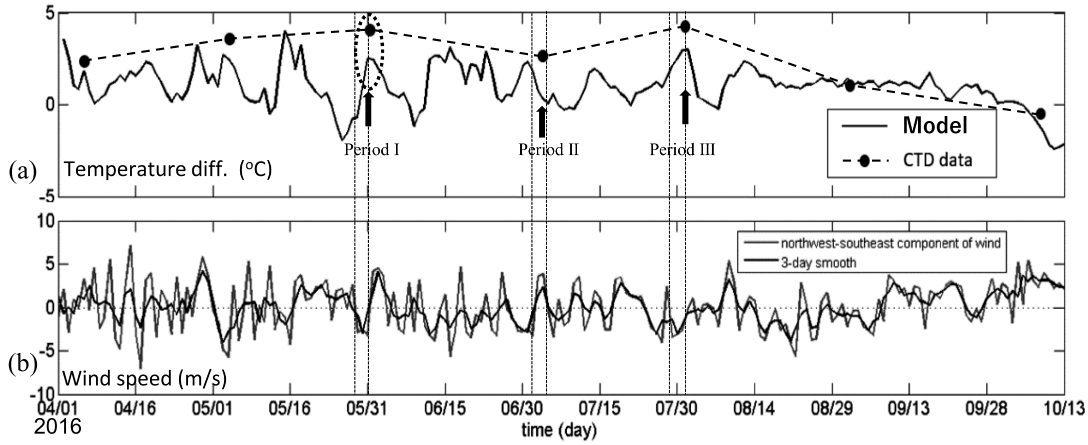

Fig. 9 (a) The time series of the difference in surface temperature between C1 and C3. The black points and solid lines are the CTD data and the model results, respectively. (b) Time series of the northwest-southeast wind component, where the gray line is the daily data, and the black line is the 3-day smoothed data. A positive wind value indicates wind blowing from the northwest.

5. Discussion

5.1 Two peaks observed in the warming season

Using Period I (May 27th to May 30th) as an example, we show how coastal water responds to the wind, in terms of horizontal and vertical distribution of water temperature and current velocity (Fig. 10). Figure 10 shows the distribution of model-derived seawater temperatures after the application of a 25-hour moving average filter, to remove the effects of the tidal cycle. According to the model, on May 27th, the wind was weak but blowing southeastward and stratification had formed in the bay. On May 28th, the wind direction became northwestward, indicating that inflow occurred within the surface layer through the narrow bay mouth. On May 29th, the northwestward wind became stronger, and the stratification in the bay almost disappeared.

The distributions of temperature and velocity for Periods I, II, and III are shown in Fig. 11. The top of Fig. 11 shows the distribution of the following day (May 30th). The inflow into the bay was weak, and the cross section shows that the water temperature stratification disappeared within the bay. The temperature inside the bay was almost uniform, at 20 °C or higher, but the thermocline was inclined, so the temperature difference between water inside and outside of the bay increased significantly. When the wind was towards the southeast, the bay water flowed out, and the coastal water responded in an almost-opposite direction, strengthening the stratification in Matsushima Bay and equalizing the SSTs of water inside and outside of the bay (Fig. 11, period II). In periods I and III, when the wind was towards the northwest, the temperature was almost vertically uniform in the bay and the SST difference between the inside and outside was large. On the other hand, in period II (southeastward wind), stratification occurred in the bay and the SST difference was small.

This demonstrates that the wind affected the variation in temperature difference between water inside and outside of the bay during the warming season. While fluctuations in winds

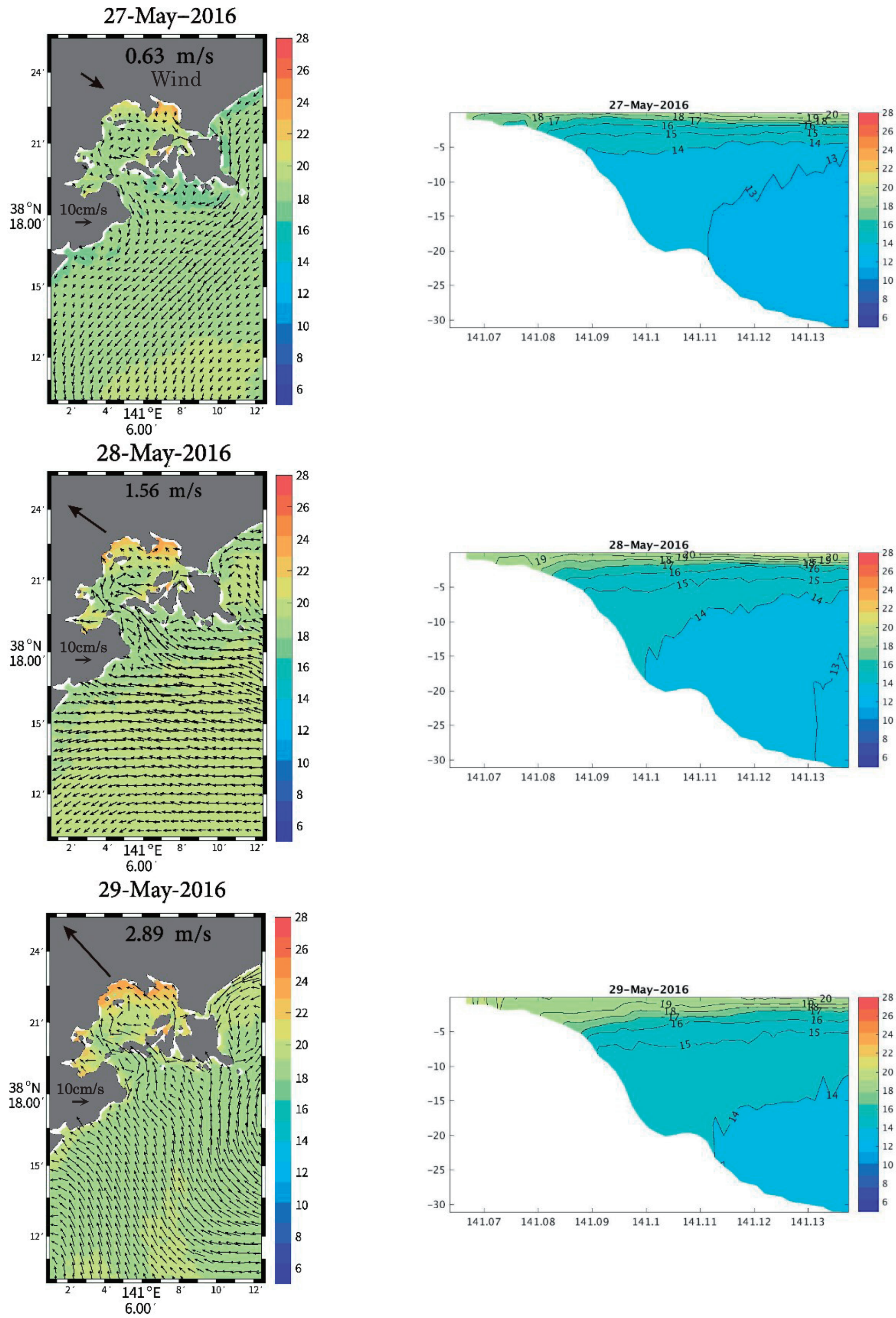

Fig. 10 Plan views (left) and vertical sections (right; taken along Line A in Fig. 7) of seawater temperature distribution between May 27th to 29th, 2016. All figures were drawn after applying a filter to the data, to remove tide effects.

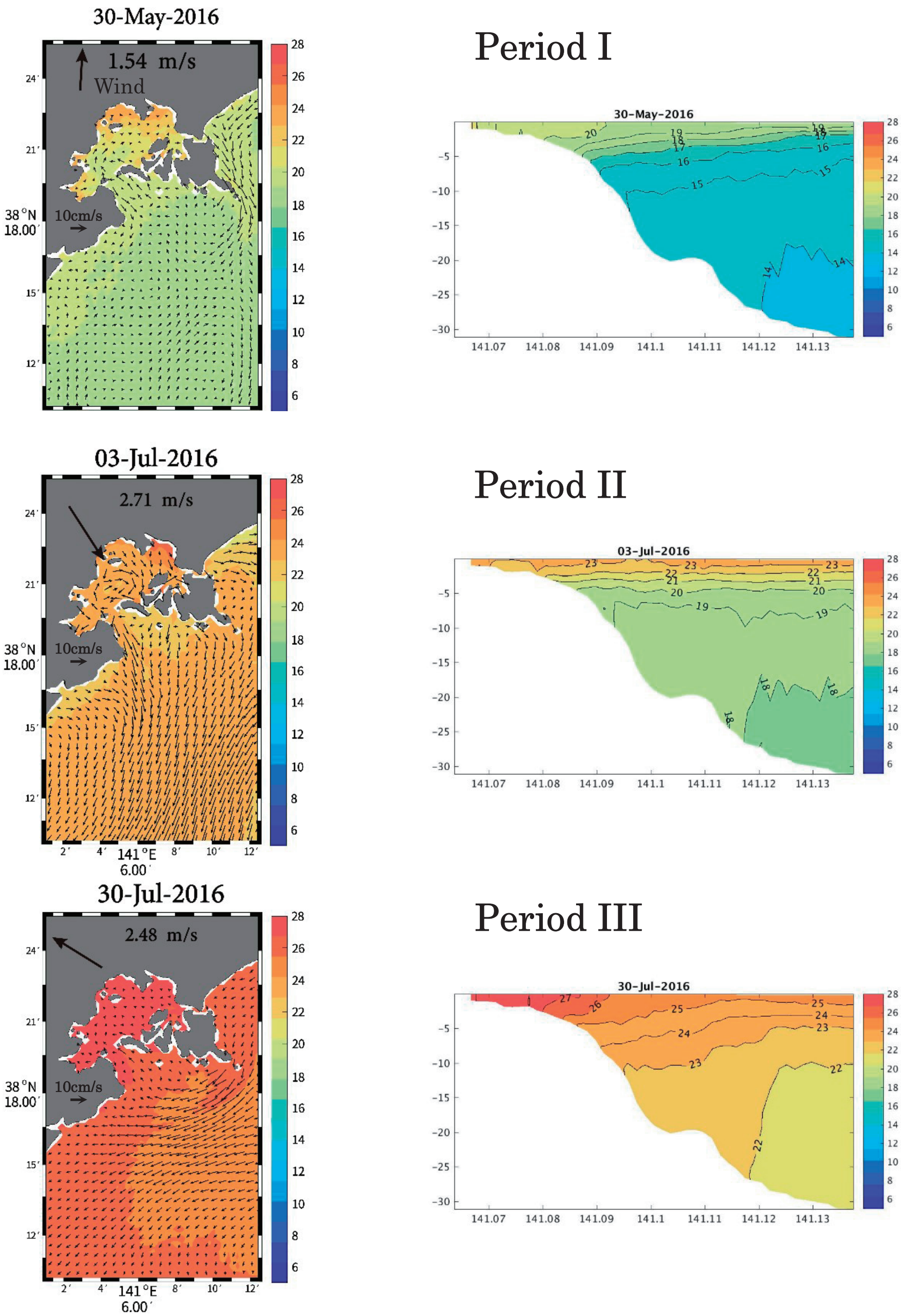

Fig. 11 Plan views (left) and vertical sections (right; taken along Line A in Fig. 7) of seawater temperature distribution for Period I, II and III. All figures were drawn after applying a filter to the data, to remove tide effects.

with several-day period cause periodical SST differences, the CTD data only obtained once in a month. The appearance of two peaks during the warming season itself is probably a type of aliasing feature. In other words, it is not important that there were two peaks, but the research conducted to investigate their characteristics revealed that wind contributes to seawater exchange in Matsushima Bay.

5.2 Relationship between tidal variation and seawater temperature

From the previous section, it is clear that stratification occurred in the bay in response to the southeastward wind. Although only the sea surface temperature was obtained by the monitoring system, it is speculated that if an internal tide variation is formed in Matsushima Bay due to the strengthening of stratification, its signal might also be captured in the SST variation. Therefore, we applied a band-pass filter, for the semidiurnal period band, to SST data obtained by the monitoring system and examined the resulting water temperature fluctuation (Fig. 12). Here, only the semidiurnal period band is extracted, so as to prevent the influence of the internal Kelvin wave of the diurnal period and/or the inertial period, which is propagating outside the region of Matsushima Bay, from being included in the data.

Semidiurnal period fluctuations were intermittently amplified at monitoring stations M1 and M3 (Fig. 12c). Here, the black lines, which indicate the amplitude of temperature fluctuation, were clearly related to wind variation (Fig. 12d). The amplification of semidiurnal temperature fluctuation appears approximately 2 days after the southeastward wind. It is reasonable to consider the amplification of the semidiurnal period fluctuation in temperature as being induced by the generation and propagation of internal tides in stratified Matsushima Bay. The model results also show amplification of the semidiurnal internal tide occurring 2 days after the southeastward wind (Fig. 12b). These results support the idea of wind-driven seawater exchange in Matsushima Bay.

5.3 Seawater exchange in Matsushima Bay

The model revealed that wind caused a change in the stratification of the bay, and the observational results also confirmed the signals of the semidiurnal internal waves. Therefore, using the model results, we calculated the seawater exchange rate caused by wind in Matsushima Bay. Table 3 shows the inflow into Matsushima Bay for Periods I, II, and III using the 25-hour running average velocity data from the bay mouth. It was found that there was an inflow of $3.5 \times 10^6 \sim 9.89 \times 10^6$ m^3/day. This flow volume becomes a flow velocity of 1.2–3.4. cm/s when the width and half-depth of the bay mouth are about 1.7 km and 2 m, respectively. While the current velocity at the bay mouth is quite small, the seawater exchange rate of Matsushima Bay over 3 days would be about 15%, and we could not ignore the effect of wind-driven seawater exchange. Namely, the wind-induced water exchange might be as much as 5% of the total volume of Matsushima Bay per day. Effect of river water was suggested to affect the water exchange in Matsushima Bay (Kakehi et al., 2017; Shirai et al., 2019). Because river water discharge was not included in this model experiment, only the effects of wind-induced seawater exchange are evaluated here. However, the effect reentering of outflow water must be considered in the case of wind-driven water exchange because a set of inflow and outflow was induced by the wind with several-day period. Since the outflow water from Matsushima Bay would be affected by the flow outside

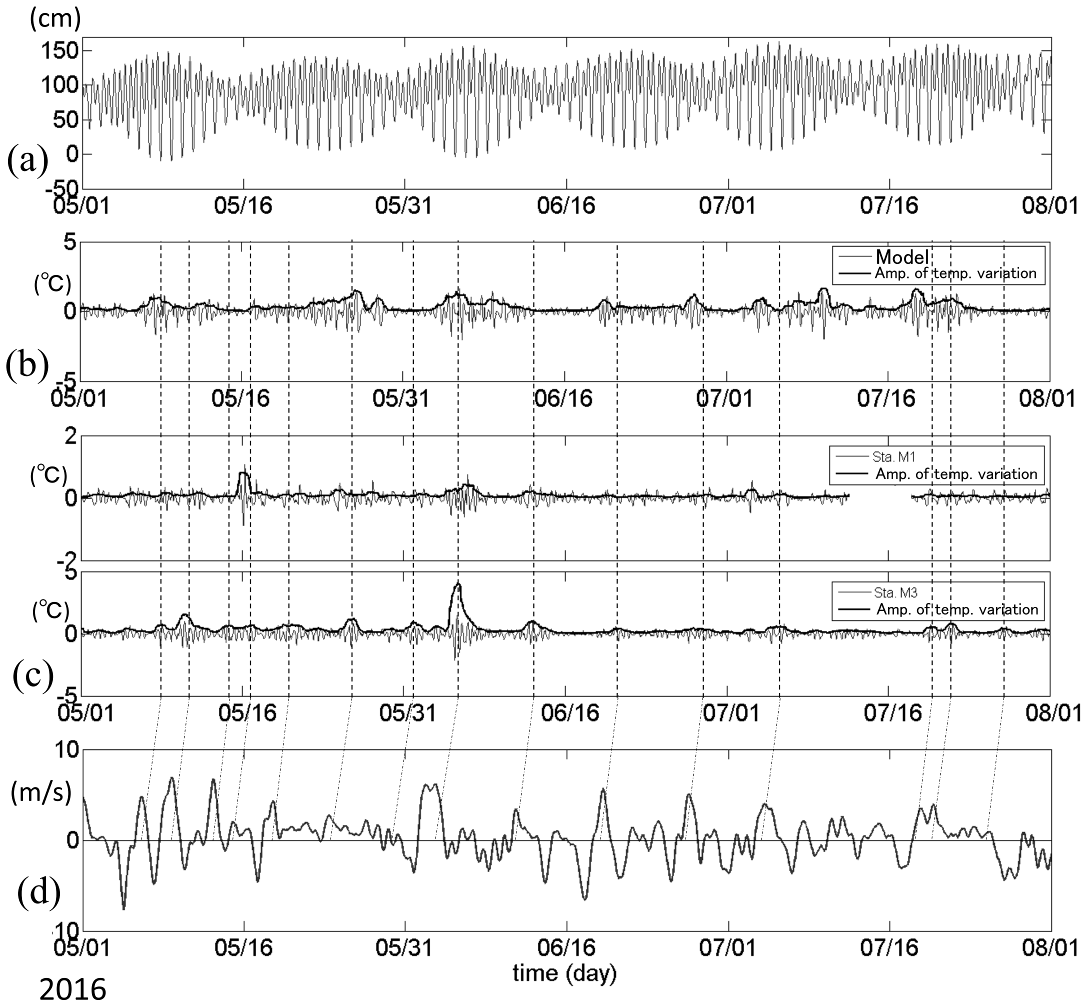

Fig. 12 (a) Time series of sea level at SIO. (b) Time series of semidiurnal band-pass-filtered temperature at M3 calculated from the model data. (c) Time series of semidiurnal band-pass-filtered SST at M1 and M3. (d) Time series of the northwest-southeast wind component. A positive wind value indicates wind blowing from the northwest.

Table 3. Inward water transport and seawater exchange rate for each period after a wind event.

Period	I		II		III	
Daily inward transport	May 28	4.36×10^6	July 1	5.59×10^6	July 28	3.76×10^6
[m^3/day]	29	4.48×10^6	2	3.50×10^6	29	4.74×10^6
	30	5.66×10^6	3	9.89×10^6	30	7.10×10^6
3-day total [m^3/day]		14.50×10^6		19.00×10^6		15.61×10^6
3-day exchange rate*		13.4 %		17.6 %		14.5 %

*3-day exchange rate = 3-day Total in follow vol./ Volume of Matsushima Bay, where volume of Matsushima Bay is about $1.08 \times 10^8 m^3$.

the Bay, it is speculated that there is little re-inflow of water into Matsushima Bay. The discussion on the re-inflow rate is left to future studies. We would like to point out in this article that per wind event, about 15% of the seawater in Matsushima Bay might be exchanged as a result of wind. More detailed investigations in the future will require appropriate arrangements of monitoring systems, and the use of reproduction models.

6. Summary and conclusion

To examine the properties of seawater exchange on Matsushima Bay, we investigated monthly temperature and salinity datasets obtained by the Miyagi Prefecture, and temperature monitoring data provided by the Sena and Varns Corporation. The difference in surface temperature, between water inside and outside of the bay, is large in early summer and late summer and decreases in mid summer. Thus, it displays two peaks in the warming season. The temperature fluctuation over a several-day period showed good correlation with the northwest-southeast component of wind, which dominated from early summer to fall. This correlation indicates that a temperature decrease is usually induced in the seawater about 2 days after the southeast wind. Furthermore, semidiurnal temperature fluctuation also becomes amplified in the bay about 2 days after the northwest wind. We employed ROMS to clarify these mechanisms, using observed atmospheric conditions and open boundary conditions. After reproducing the temperature variation from spring to fall, we found that over a several-day period, wind could induce water exchange and variation in the temperature difference between water inside and outside of Matsushima Bay.

The temperature difference between water inside and outside of Matsushima Bay was expected to reach a maximum in midsummer; however, it was reduced in July. This was thought to be related to seawater exchange. Combining SST data obtained by the monitoring system, and wind data from AMEDAS, we found that there was a strong correlation between the SST in Matsushima Bay and the southeast-northwest component of the wind. When the wind blew from the southeast, the temperature difference was large. The model indicates that the southeast wind transports warm surface water into the bay, and the northwest wind contributes to the formation of stratification in Matsushima Bay. It was clarified that the wind affected the change in temperature difference during the warming season. Furthermore, the model results revealed that the SST difference between water inside and outside of the bay was frequently induced by wind fluctuation. The appearance of two peaks during the warming season itself is thought to be a type of aliasing feature. Thus, the that there were two peaks is not necessarily important, but research conducted to investigate their characteristics has revealed that wind contributed to seawater exchange in Matsushima Bay. This study showed that small bays such as Matsushima Bay can undergo large changes in sea conditions in a relatively short time. The continuous monitoring system used in this study is very effective tool for accurately gathering data on physical phenomena, such as seawater exchange.

Furthermore, the model results suggest the generation and propagation of internal waves during the period of temperature stratification in Matsushima Bay. From the surface temperature data obtained in the bay, we found that semidiurnal fluctuations were intermittently amplified about 2 days after the southeastward wind blew. This supported our idea that wind could induce seawater exchange and subsequent stratification of Matsushima Bay. In addition, it was shown that wind-induced seawater exchange could move 15% of the volume of Matsushima Bay in 3 days, making it a non-negligible mechanism of seawater exchange in the bay. However, there are some unresolved questions, especially regarding quantitative reproducibility of the details of seasonal variation by the model, and further investigation is needed. To increase the accuracy of the simulation, the influence of rivers must be taken into account. More observation data is required to clarify the effect of internal waves on water mixing.

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Preliminary analysis of sablefish (*Anaplopoma fimbria*) otolith measurements from Northern Pacific in 1984

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Abstract: Sablefish otoliths (sagittae) collected from four areas (Northern California, Gulf of Alaska, Bering Sea, and Aleutian Islands) in 1984 were used to determine age by the section otolith aging method, and to measure otolith radius and thickness. The relationship between otolith ratio (radius/ thickness) and age was linear in the four areas. There was no statistical difference in the comparison of the age-otolith ratio relationship between the Gulf of Alaska, Bering Sea and Aleutian area; however, that of Northern California was found to be significantly different from the other three. These results are in keeping with the two-population hypothesis of previous tagging studies. Thus, sablefish otolith measurements might be a sensitive characteristic for discerning sablefish population structures. Further studies of otolith morphometric analysis including shape might provide an even clearer picture of sablefish populations.

Keywords : *Sablefish, otolith measurements, North Pacific*

1. Introduction

The sablefish, or black cod, *Anoplopoma fimbria* (Pallas), is one of the commercially important Pacific coast groundfish species, inhabiting the continental shelf and slope from Baja California through the Bering Sea to Kamchatka and northern Japan (HART, 1973; SASAKI, 1985). Results of analysis of sablefish tag-recapture growth data suggest that there may be at least two populations of sablefish: an Alaska population ranging from the Bering Sea and Aleutian waters extending down through the Gulf of Alaska to northwest Vancouver Island, Canada; and a west-coast population extending from southwest Vancouver to Baja California (KIMURA *et al.* 1998; MALONEY and SIGLER, 2008). Here we made a preliminary analysis of age-otolith measurements using specimen from four areas (Northern California, the Gulf of Alaska, Bering Sea and Aleutian Islands) to determine whether otolith measurements provide a clue as to differences in sablefish populations.

2. Materials and Methods

Sablefish otolith samples collected by bottom trawl vessels in Northern California from April to August in 1984, and by bottom longline vessels under the US-Japan Joint Survey ranging from the Gulf of Alaska and Aleutian Islands to the Bering Sea from June to September in 1984, were used to determine age using the section ag-

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Table 1. Sample sizes and ranges of fork length (cm) of sablefish age and otolith measurements, ranges of age assignments from the section aging methods for sablefish collected by bottom longline in the Gulf of Alaska, Aleutian Islands, and Bering Sea in 1984 and by bottom otter trawl in Northern California in 1984.

Area	Female otolith ages and measurements		
	Sample Size	Length Range (cm)	Section age range (year)
Gulf of Alaska	942	43–99	3–42
Aleutian Islands	418	46–106	2–48
Bering Sea	600	44–99	2–50
Northern California	305	37–90	1–22
Total	2265	37–106	1–50

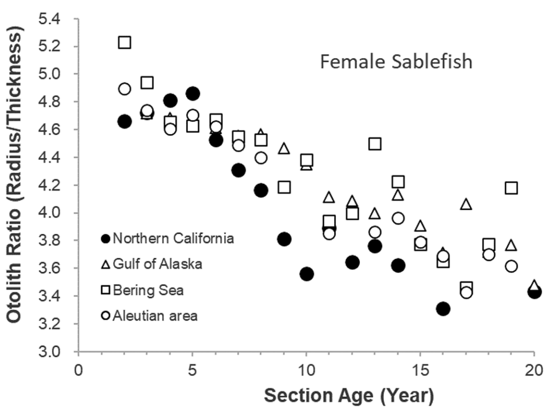

Fig. 1 Mean otolith ration (otolith radius/otolith thickness) -age relationship of female sablefish, using otolith collected in Northern California, Gulf of Alaska, Bering Sea and Aleutian Islands in 1984.

ing method (BEAMISH and CHILTON, 1982) and measure otolith radius and thickness by ocular meter of dissecting microscope in O.U. (Ocular Unit). Only female data were used for the analysis. Mean otolith ratio (otolith radius/otolith thickness) was linearly related to section age, and linear model parameters were obtained by least-squares analysis. As the number of data was limited, we used samples only in the age range of 2–20 years and more than three data at an age to estimate linear model parameters. All presented statistical tests were performed at the 5% significance level to compare age-otolith ratio relationships for the four sites.

3. Results

A total of 2,265 sablefish otoliths collected in 1984 were successfully aged by section methods (Table 1). The assigned section age ranged from 1–50 years. In Northern California, the maximum age was 22, much younger than in the other three areas.

Mean otolith ratio (otolith radius/otolith thickness) decreased in a linear fashion with section age from four different areas (Fig. 1). The use of regression analysis to establish the relationships between otolith ratio and section age showed that otolith ratio was highly correlated with section age for females for each area (Table 2).

The fitted regression lines were compared among areas. Variances among four areas were found to be heteroscedastic, using Bartlett's test of homogeneity of variance ($\chi 2 = 9.227$, df = 3). Analysis of covariance (ANCOVA) techniques were used to compare otolith ratio-section age relationships by pairwise. There were no significant differences between regressions in the Gulf of Alaska, Bering Sea and Aleutian Islands, however the regression from Northern California

Table 2. Slopes, intercepts, and correlation coefficients (r) for regression lines relating mean otolith ratio (radius/thickness) to section age for female sablefish, using otoliths collected in the Gulf of Alaska, Aleutian area, Bering Sea, and Northern California in 1984.

Area	Female		
	Slope	Intercept	r
Gulf of Alaska	−0.070	5.010	−0.962
Bring Sea	−0.074	4.992	−0.936
Aleutian Islands	−0.077	4.992	−0.969
Northern California	−0.096	4.969	−0.909

Table 3. Summary of comparison of slope and intercepts of regression line for otolith ratio (otolith radius/otolith thickness) to section age for female sablefish, using otoliths collected in the Gulf of Alaska, Bering Sea, Aleutian Islands, and Northern California in 1984.

Hypothesis	Test	Slope			Intercept		
		statistics	df	Result	statistics	df	Result
Northern California vs Gulf of Alaska	F	2.045	1,29	Accept	20.907	1,31	Reject
Northern California vs Bering Sea	F	0.207	1,25	Accept	13.436	1,27	Reject
Northern California vs Aleutian Islands	F	0.934	1,27	Accept	14.251	1,29	Reject
Gulf of Alaska vs Bering Sea	F	1.176	1,28	Accept	0.077	1,30	Accept
Gulf of Alaska vs Aleutian Islands	F	0.627	1,30	Accept	1.323	1,32	Accept
Bering Sea vs Aleutian Islands	F	0.250	1,26	Accept	0.218	1,28	Accept

was highly significantly different from the other three (Table 3).

4. Discussion

Knowledge regarding the population structure of a species is essential to effectively assess and manage fisheries. Sablefish are widely distributed along the North Pacific Ocean from the Aleutian Islands and Bering Sea to Baja California (SASAKI, 1985). For the wide distribution of sablefish, tag release-recovery studies have revealed that at least two populations potentially exist along the coast of north America: one extending northwest from northern Vancouver Island thorough the Gulf of Alaska, Aleutian Islands, and the Bering Sea; and the other extending south from southwest Vancouver Island to Baja California (KIMURA *et al.*, 1998). Results of this preliminary analysis of sablefish otolith morphometrics implies the possibility of stock separation. Further sablefish otolith morphometrics analysis may expose a much clearer population structure. Otolith morphometrics, including shape analysis, are widely used in studies to separate populations for different species, for example, horse mackerel, *Trachurus trachurus* (ABUANZA *et al.*, 2008), cod, *Gadus morhus* (STRANSKY *et al.*, 2008), and Pacific sardine, *Sardinops sagax* (JAVOR *et al.* 2011).

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