

## Molecular and biological studies of nonindigenous and extremely rare fish species from the western Baltic reported from the Pomeranian Bay (southwest Baltic Proper)

Beata WIĘCASZEK , Remigiusz PANICZ , Piotr ELJASIK , ADAM TAŃSKI  and Amin BUSHRA

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Water inflows from the North Sea to the Baltic Sea are recognized as a significant factor influencing the diversity of fish species in the region. In this report, we present findings on three newly discovered fish species (*Solea solea*, *Merluccius merluccius*, and *Limanda limanda*) and the presence of species that were previously seldom observed in the Pomeranian Bay and the associated oligohaline waters of Szczecin Lagoon. These fishes were incidentally captured during monitoring surveys of commercially important fish species. Species identification relied on partial sequences of cytochrome c oxidase subunit I (*COI*), cytochrome b (*cytb*), and rhodopsin (*rho*) genes, as well as morphometric diagnostic characteristics. Upon comparing the obtained sequences with GenBank records, it was revealed that the sequences for *Merluccius merluccius* (*rho*, GenBank acc. no. OM737733) and *Chelidonichthys lucerna* (*cytb*, GenBank acc. no. OM737734) constitute new DNA barcodes. The majority of sequences obtained in our study matched those available in GenBank for fishes inhabiting the North Sea, suggesting spatial and temporal linkages between the two seas. The remaining sequences exhibited similarity to data from the Cantabrian Sea, the coasts of France, and the Norwegian Sea. The study results, in conjunction with information on the inflows of saline waters and data from previous studies on reported fish occurrences, indicate that the bycatch species could serve as potential bioindicators of environmental changes in the study area.

Key words: biodiversity, bycatch, climate change, North Sea, water inflows.

WIĘCASZEK Beata, TAŃSKI Adam, Department of Hydrobiology, Ichthyology and Biotechnology of Breeding, Faculty of Food Sciences and Fisheries, West Pomeranian University of Technology in Szczecin. PANICZ Remigiusz, ELJASIK Piotr , Department of Meat Science, Faculty of Food Sciences and Fisheries, West Pomeranian University of Technology in Szczecin.

E-mail: peljasik@zut.edu.pl

BUSHRA Amin, Mirza Ghalib College, Magadh University, Gaya, Bihar, India

The Baltic Sea is an extensive, brackish, semi-enclosed sea significantly impacted by climate fluctuations. The ongoing climate change in northern Europe is anticipated to influence both the temperature and salinity of the Baltic, leading to a warmer and less saline environment (Reusch *et al.* 2018; McKenzie *et al.* 2021). Furthermore, this shift in temperature and salinity could instigate alterations in biogeography and ecosystem functioning (Frainer *et al.* 2017).

Direct consequences of climate change will be evident in crucial hydrographic characteristics, such as the properties of saline water inflow from the North Sea to the Baltic. This influence will occur both through atmospheric forcing and indirectly through modified salinity dynamics (Lehmann *et al.* 2022). Hydrographic processes affecting salinity will exert rapid and diverse impacts on species distributions within the Baltic Sea. Projections suggest that cer-

tain marine species may immigrate due to anticipated increases in sea temperature. However, only a limited number of these species are expected to successfully colonize the Baltic due to its low salinity (MacKenzie *et al.* 2007). Escalating temperatures will disrupt seasonal cycles, rendering some habitats more or less suitable. Consequently, species may adapt to new conditions, either phenotypically or evolutionarily, shift their ranges, or face extinction. Observations of phenological, distributional, and genetic changes in response to climate change have already been documented across a broad spectrum of taxa, including fishes (Frost *et al.* 2012; Fraimer *et al.* 2017). As climate change progresses, novel communities will emerge as species with differing dispersal abilities, environmental tolerances, and genetics respond individually to these environmental shifts (Walther 2010).

The Baltic Sea is acknowledged for harboring a fish and lamprey community with relatively few species, estimated at around 200 (Ojaveer *et al.* 2010). However, if the Kattegat is excluded, the count diminishes to approximately 100 established species (Ojaveer *et al.* 2010). The primary factor contributing to this low species richness is the Baltic's diminished salinity, inducing physiological stress in both freshwater and marine species (Ojaveer & Kalejs 2005). Key commercial species, including cod (*Gadus morhua* L.), herring (*Clupea harengus* L.), sprat (*Sprattus sprattus* L.), salmon (*Salmo salar* L.), and sea trout (*Salmo trutta* L.), are subject to monitoring in all Baltic countries. As these surveys inadvertently capture a variety of other species as bycatch, they have the potential to be utilized for monitoring alterations in the overall diversity of fish species, such as those resulting from fishing, species introductions, and climate change (Ojaveer *et al.* 2010).

Monitoring surveys conducted from 2007 to 2010 and 2011 to 2019 in the Pomeranian Bay (PB) focused on commercial species, notably cod, herring, sprat, European flounder *Platichthys flesus* (L.), pikeperch *Sander lucioperca* (L.), and perch *Perca fluviatilis* L. (Dudko *et al.* 2015). The PB, located in the Bornholm Basin (ICES SD 24) near the Arkona Basin and Eagle Bank, is a shallow basin off the coasts of Poland and Germany with a depth not exceeding 30 m. In the bottom layers, the salinity ranges from 7.2 to 7.6 (mean 7.4), while at the surface layers, it varies from 3.9 to 7.3 (mean 6.2) (Abbas *et al.* 2015). This region is characterized by water mixing influenced by two key factors: riverine water input and water exchange with adjacent open seawaters, affecting the hydrological conditions of the area (Beszczyńska-Möller 1999). To date, 56 fish and two

lamprey species have been documented in this area, with 35 being marine, 13 freshwater, and 10 diadromous (Więcaszek *et al.* 2019). The bay receives inflows that typically range from oligohaline (salinity about 1-3) to freshwater from the Szczecin Lagoon through three outlets (Radziejewska & Schernewski 2008).

The central focus of this study was to determine whether the presence of new, exceptionally rare, or nonindigenous fish species (identified incidentally during monitoring surveys of commercial fish species) could indicate environmental changes in the PB. We examined the correlation between the occurrence of rare fish species in the coastal zone of the PB and the influx of saline North Sea water into the Baltic, utilizing both our own data and information from existing literature.

## Material and Methods

### Ichthyological study

The fishes examined in this study were captured incidentally as bycatch during monitoring surveys of commercial fish species in the PB (southwest Baltic Proper, ICES SD 24). These catches were carried out four times a year in May, September, November, and December, spanning from 2011 to 2019. The surveyed area encompassed approximately 0.18 km<sup>2</sup> of the seafloor in one haul (two hauls per cruise). Fishing activities were conducted using trawls (mesh size of 10-20 mm) from the research vessel SNB-AR-1 at depths ranging from 9.8 to 14.6 m. The commercial fish surveys followed routes at 53°57'N to 54°10'N and 14°19'E to 14°47'E. Additionally, one specimen was captured in the northern part of Szczecin Lagoon (53°48'N; 14°22'E) using a roach fyke net and was transported to the laboratory by a local fisher. The collected fishes underwent measurements to the nearest millimeter, weighed to the nearest 0.1 g, and sex was determined macroscopically (Table 1). Basic metric and meristic measurements were taken for each specimen to facilitate species identification (Whitehead *et al.* 1986; Cohen *et al.* 1990; Lloris *et al.* 2005; Froese & Pauly 2022). To explore the correlation between the periodic occurrence of rare fish species in the PB and the influx of saline waters from the North Sea, a literature review was conducted. Data from earlier studies, combined with our results, are presented in Figure 1 and Table 2.

Table 1

Detailed data on non-indigenous and rare migrant fish species recorded in the Pomeranian Bay and Szczecin Lagoon 2011-2019 (this study) and in 1996-2018 (data from literature)

Species and its taxonomic status	Total length TL [mm], weight of fish [g] and sex	Status in HELCOM Red List**	Collection date and number of specimens [if known]	References
Gadidae: <i>Merlangius merlangus</i> (L., 1758)	255 mm, 122 g ♂	VU	24 Nov. 2015	This study
		RA	2015	Dudko <i>et al.</i> 2015
Gadidae: <i>Pollachius virens</i> (L., 1758)*	262 mm, 141.51 g immature	NA	15 Sept. 2018*	This study
		NE	1996	Krzykawski <i>et al.</i> 2001
Merluccidae: <i>Merluccius merluccius</i> L., 1758)	555 mm, 1650 g ♂	NT	24 Nov. 2015	This study
Triglidae: <i>Chelidonichthys lucerna</i> (L., 1758)	299 mm, 261.6 g ♂	NA	15 Dec. 2013	This study
	320 mm, 282 g ♂		24 Nov. 2015	
	383 mm, 650.7 g ♀		24 Nov. 2015	
	366 mm, 455.7 g ♀		29 Dec. 2016	
	355 mm, 477.9 g ♀		29 Dec. 2016	
		NA	1998; 1 1999; 1 2007; 1	Więcaszek <i>et al.</i> 2011 Więcaszek <i>et al.</i> 2011 Więcaszek <i>et al.</i> 2019
Mullidae: <i>Mullus surmuletus</i> L., 1758	219 mm, 122.8 g ♀	NE	20 Sept. 2011	This study
	225 mm, 132.3 g ♀	RA	24 Nov. 2015	
		NE	2007; 1	Więcaszek <i>et al.</i> 2011
Scombridae: <i>Scomber scombrus</i> L., 1758	500 mm, 1100 g ♀	NA	20 May 2016	This study
	520 mm, 1110 g ♀			
	480 mm, 985.5 g ♀	NA	2012, 2013 2018; 1	Dudko <i>et al.</i> 2015 Deconinck <i>et al.</i> 2020
Scophthalmidae: <i>Scophthalmus rhombus</i> (L., 1758)	337 mm, 597.7g ♀	RA	23 Nov. 2018	This study
	272.5 mm, 290.9g ♂		20 May 2019	
		RA	2014; 2	Więcaszek <i>et al.</i> 2019
Pleuronectidae: <i>Limanda limanda</i> (L., 1758)	301 mm, 412g ♀***	RA	23 Nov. 2018	This study
	293 mm, 286g ♀			
Soleidae: <i>Solea solea</i> (L., 1758)	275 mm, 210 g ♀	RA	30 May 2017	This study
	265 mm, 196.5 g ♀		20 May 2019	

\* Szczecin Lagoon;

\*\* Symbols of HELCOM Red List: NE – Not Evaluated; NT – Near threaten; VU – Vulnerable; NA – not applicable; RA – rare

\*\*\* Left-sided specimen.

### Molecular study

Upon arrival at the laboratory, muscle samples were collected from all fish specimens for DNA extraction, performed using the High Pure PCR Template Preparation Kit (Roche) following the manufacturer's instructions. The quality and quantity of

DNA isolates were evaluated through separation in a 1.5% agarose gel and spectrophotometric measurements using a NanoDrop 2000 (Thermo Scientific). Standard barcoding primers and temperature profiles were employed to amplify cytochrome oxidase subunit I (*COI*), rhodopsin (*rho*), or partial cytochrome b

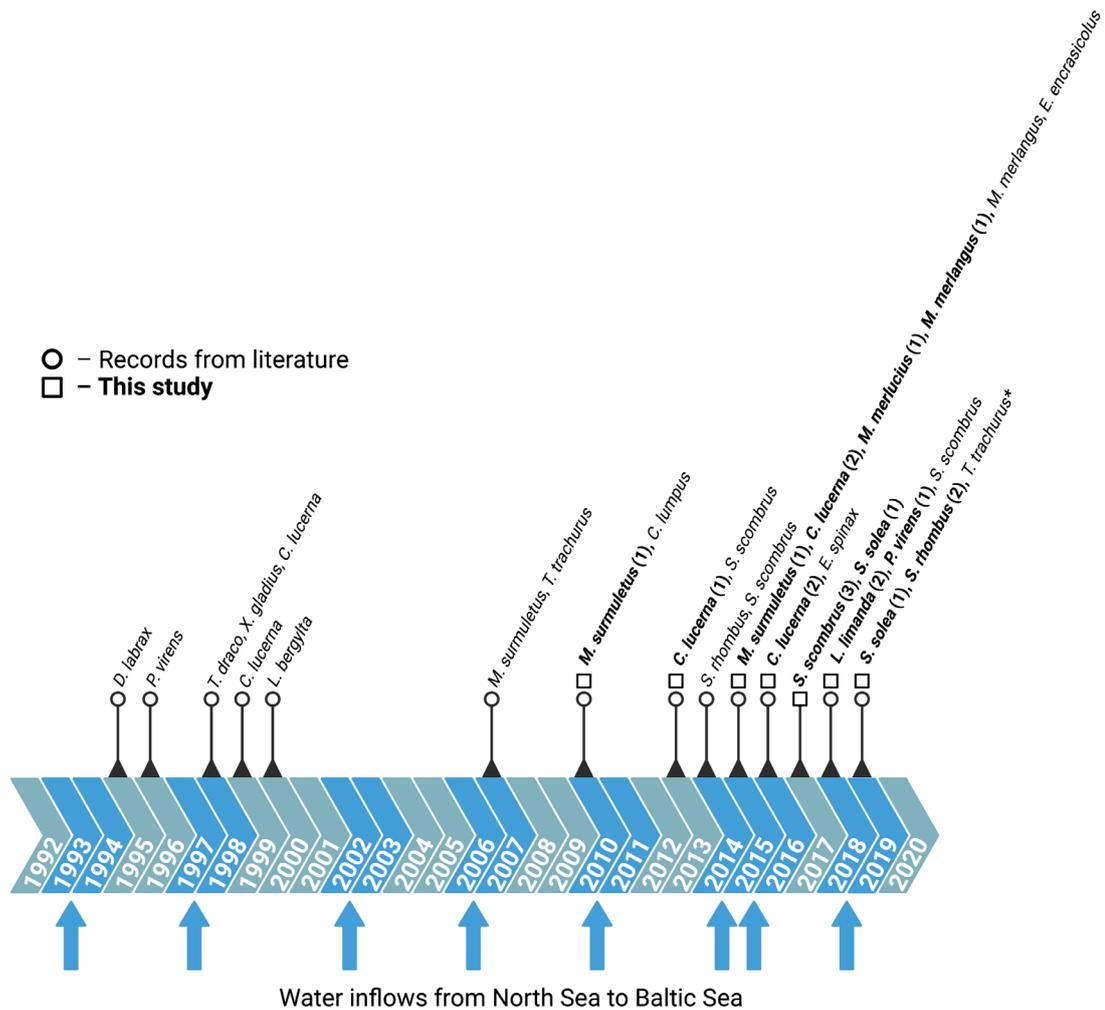


Fig. 1. Timeline illustrating medium and large inflows of saline water from the North Sea into the Baltic Sea (arrows) and occurrences of rare and non-indigenous fish species in the Pomeranian Bay from 1993 to 2019. Fish names noted in this study are in bold, and the number of specimens is indicated in brackets; \* own data, unpublished; information on inflows of saline water from the North Sea into the Baltic Sea was compiled from [Mohrholz \(2018\)](#); [Naumann \*et al.\* \(2017a\)](#); [Copernicus Marine Service \(2021\)](#).

Table 2

Detailed data from the literature on non-indigenous and rare migrant fish species recorded in the Pomeranian Bay and Szczecin Lagoon, in 1995-2017

Species and its taxonomic status	Date of catch; number of specimens	References
Etmopteridae: <i>Etmopterus spinax</i> (L., 1758)	2017; 1	<a href="#">Więcaszek <i>et al.</i> 2018</a>
Engraulidae: <i>Engraulis encrasicolus</i> (L., 1758)	2015	<a href="#">Dudko <i>et al.</i> 2015</a>
Cyclopteridae: <i>Cyclopterus lumpus</i> L., 1758*	April 2010; 1	<a href="#">Więcaszek <i>et al.</i> 2015</a>
Mugilidae: <i>Chelon labrosus</i> (Risso, 1827)	November 2007 June 2008 Szczecin Lagoon; 1	<a href="#">Czerniejewski <i>et al.</i> 2008</a> , <a href="#">Więcaszek <i>et al.</i> 2011</a>
Carangidae: <i>Trachurus trachurus</i> (L., 1758)	30 September 2007; 2 juveniles; 20 May 2019; own observation; 1 juvenile	<a href="#">Więcaszek <i>et al.</i> 2011</a>
Moronidae: <i>Dicentrarchus labrax</i> (L., 1758)	9 September 1995; 1	<a href="#">Krzykawski <i>et al.</i> 2001</a>
Trachinidae: <i>Trachinus draco</i> L., 1758	December 1998; 1	<a href="#">Krzykawski <i>et al.</i> 2001</a>
Labridae: <i>Labrus bergylta</i> Ascanius 1767	December 2000; 1	<a href="#">Keszka &amp; Raczyński 2002</a>
Xiphiidae: <i>Xiphias gladius</i> L., 1758	4 September 1998; 1	<a href="#">Krzykawski <i>et al.</i> 2001</a>

\*total length of *C. lumpus* (42.7 cm) indicates the North Sea origin.

(*cytb*) regions through end-point PCR (Ward *et al.* 2005; Sevilla *et al.* 2007). Amplifications were carried out on a T100™ Thermal Cycler (Bio-Rad) using the GoTaq PCR kit (Promega). The reaction mix included 5 µl of Green GoTaq® Flexi Buffer, 2.5 µl of MgCl<sub>2</sub> (25 mM Solution), 0.5 µl of PCR Nucleotide Mix (10 mM), 0.125 µl of GoTaq® DNA Polymerase (5 u µl<sup>-1</sup>), 0.5 µM of each primer, and 2 µl of DNA template in a final volume of 25 µl. The raw reads of PCR products were assembled using Geneious 8.0 (Kearse *et al.* 2012) and compared against GenBank sequences using BLAST (Altschul *et al.* 1990) to confirm the species of the specimens. All obtained sequences are provided in the supplement (Supplementary Materials SM.01.).

**Results**

Ichthyological study

A total of 19 fish specimens representing nine species underwent examination, with 18 caught in the PB and one saithe individual, *Pollachius virens*, caught in the Szczecin Lagoon. Detailed morphological characteristics of taxonomic significance for whiting (*Merlangius merlangus*), saithe, European hake (*Merluccius merluccius*) (Table 3), tub gurnard (*Chelidonichthys lucerna*) (Table 4), surmullet (*Mullus surmulletus*) (Table 5), Atlantic mackerel (*Scomber scombrus*), dab (*L. limanda*), brill (*Scophthalmus rhombus*), and common sole (*Solea solea*) (Table 6) confirmed the initial species identification and align

Table 3

Morphological characters of taxonomic significance for gadoids: *Merlangius merlangus*, *Pollachius virens*, and *Merluccius merluccius*

Character	<i>Merlangius merlangus</i> n = 1	<i>Pollachis virens</i> n = 1	<i>Merluccius merluccius</i> n = 1
Meristic characters			
D <sub>1</sub> – ray count in first dorsal fin	14	16	10
D <sub>2</sub> – ray count in first dorsal fin	19	22	39
D <sub>3</sub> – ray count in first dorsal fin	26	23	–
A <sub>1</sub> – Anal rays count	37	27	37
A <sub>2</sub> – Anal rays count	22	21	–
P – Pectoral rays count	19	–	14
V – Ventral rays count	6	–	1/7
GR <sub>1</sub> – Gill rakers count (in two rows)	–	–	10/9
Metric characters expressed as % of SL			
SL – standard length	[229 mm]	[240 mm]	[503 mm]
HL – length of head	28.9	26.3	29.8
H – maximum body depth	20.5	21.3	17.9
h – minimum body depth	5.7	5.4	4.6
D1-D2 – distance between fins	3.0	2.7	2.4
laco – width of body	9.8	12.9	16.4
Metric characters expressed as % of HL			
lmd – length of lower jaw	35.4	38.1	58.7
lmx – length of upper jaw	36.9	–	46.3
Oh – eye diameter	21.5	19.1	15.3
iO – interorbital length	30.8	30.27	21.3
hc – head height	53.8	60.91	46.0
lac – head width	34.6	42.9	52.7
Peculiar diagnostic characters for the species	Anal fins touching each other or nearly so; 1.7% SL	Very small chin barbel; lateral line smooth along its entire length	Scales present on nasal membrane, lower part of cheek, and lacrimal

Table 4

Morphological characters of taxonomic significance of *Chelidonichthys lucerna* (n = 5)

Metric characters in % of standard length SL		Metric characters in % of head length HL	
HL – length of head	29.3	pO – preorbital length	50.6
Hc – height of head	15.2	poO – postorbital length	30.9
H – maximum body depth	18.1	hc – height of head	52.0
h – minimum body depth	4.9	Oh – eye diameter	19.7
IP – length of pectoral fin P	34.6	lmd – length of lower jaw	40.8
hD <sub>1</sub> – depth of first dorsal fin	15.6	lmx – length of upper jaw	40.8
hD <sub>2</sub> – depth of second dorsal fin	11.9	lac – width of head	46.4
hA – depth of anal fin	9.9	length of spine	22.5
V-A distance between V-A bases	32.9	Meristic characters	
P-V distance between P-V fin bases	16.8	D <sub>1</sub> – ray count in first dorsal fin	VIII
ID <sub>2</sub> bs – length of second dorsal fin base	36.2	D <sub>2</sub> – ray count in first dorsal fin	I, 14
lAbs – length of anal fin base	31.3	A – Anal rays count	I, 15
pA – preanal length	55.6	P – Pectoral rays count	10 + III
pD <sub>1</sub> – predorsal length	30.0	V – Ventral rays count	I, 5
pD <sub>2</sub> – predorsal length	49.8	GR <sub>1</sub> – count of rakers on 1 <sup>st</sup> gill arch – first row	17
pV – preventral length	26.3	GR <sub>1</sub> – count of rakers on 1 <sup>st</sup> gill arch – second row	11

Table 5

Morphological characters of taxonomic significance of *Mullus surmuletus* (n = 2)

Metric characters in % of standard length SL	% SL	Metric characters in % of head length HL	% HL
TL – total length	125.4	Max. head depth (at ventral edge of operculum)	79
HL – length of head	28.66	Head depth across vertical mid-line through eye	62.5
HEAD <sub>1</sub> – height of head at D <sub>1</sub>	24.13	SUBORB – suborbital depth	43.33
BARBL – length of barbel	26.66	iO – interorbital length	45
pD – predorsal length	35.05	lmx – length of upper jaw	31.46
pV – preventral length	31.76	lmd – length of lower jaw	40.62
pA – preanal length	62.15	BARBL – barbel length	72.1
IP – length of pectoral fin	20.90	BARBW – maximum barbel width	2.92
IPbs – length of pectoral fin base	6		
IV – length of pelvic fin	22.51		
IVbs – length of pelvic fin base	3.05	Meristic characters	
P-A – distance between P-A fin bases	33.97	D <sub>1</sub> – ray count in first dorsal fin	VII
P-V – distance between P-V fin bases	10.6	D <sub>2</sub> – ray count in second dorsal fin	I, 7
V-A – distance between V-A bases	35.70	A – Anal rays count	I, 6
hD <sub>1</sub> – depth of first dorsal fin	20.54	P – Pectoral rays count	17
hD <sub>2</sub> – depth of second dorsal fin	14.68	V – Ventral rays count	I, 5
D <sub>1</sub> -D <sub>2</sub> – distance between fins	8.98	GR <sub>1</sub> – count of rakers on 1 <sup>st</sup> gill arch	21
ID <sub>1</sub> bs – length of first dorsal fin base	19.62	GR <sub>2</sub> – count of rakers on 2 <sup>nd</sup> gill arch	14
ID <sub>2</sub> bs – length of second dorsal fin base	16.29		
hA – depth of anal fin	15.43		
lAbs – length of anal fin base	11.51		
H – maximum body depth	26.24		
h – minimum body depth	9.89		
lpc – length of caudal peduncle	25.16		
laco – width of body	20.70		

Table 6

Morphological characters of taxonomic significance for *Scomber scombrus* and flatfish: *Scophthalmus rhombus*, *Limanda limanda*, and *Solea solea*

Character	<i>Scomber scombrus</i> n = 3	<i>Scophthalmus rhombus</i> n = 2	<i>Limanda limanda</i> Left-sided n = 1	<i>Limanda limanda</i> Right-sided n = 1	<i>Solea solea</i> n = 2
Meristic characters					
D <sub>1</sub> – Dorsal rays	XI-XII	79-80	69	68	80
D <sub>2</sub> – Dorsal rays	II, 9-10+5	–	–	–	–
A <sub>1</sub> – Anal rays	II, 9-10 +5	57-58	56	61	63
P – Pectoral rays	I, 18	12-13	10	10	9-10
V – Ventral rays	I, 5	6	6	6	6
Metric characters expressed as % of SL					
SL – standard length	[410-425 mm]	[202-275 mm]	[293 mm]	[301 mm]	[237, 246 mm]
HL – length of head	26.5-24.5	30.9-32.4.02	20.0	20.8	19.4-19.1
H – maximum body depth	19.1-19.3	66.0-68.3	41.6	43.5	39.2-38.2
h – minimum body depth	3.3-3.5	13.5-14.4	8.1	10.1	8.4-8.1
D <sub>1</sub> – fin groove	13.3-15.1	–	–	–	–
D <sub>2</sub> bs – base of D <sub>2</sub> fin	11.1-10.6	–	–	–	–
D <sub>1</sub> -D <sub>2</sub> – space between D <sub>1</sub> and D <sub>2</sub> fin groove	17.1-21.4	–	–	–	–
D <sub>1</sub> -D <sub>2</sub> % – space between D <sub>1</sub> and D <sub>2</sub> in % of D <sub>1</sub> fin groove	129.1-142.8	–	–	–	–
Metric characters expressed as % of HL					
lmd – length of lower jaw	–	51.2-55.0	41.6	47.2	29.3-30.4
lmx – length of upper jaw	–	45.9	27.9	28.0	31.5-29.8
Oh – eye diameter	–	16.0-16.5	27.4	24.3	18.5-20.2
iO – interorbital length	–	13.7-16.5	8.6	8.8	11.7
Peculiar diagnostic characters for the species	Swim bladder absent; space between D <sub>1</sub> and D <sub>2</sub> clearly greater than fin groove	Eyed-side without bony tubercles	Lateral line forms a distinct curve above P fin	Lateral line forms a distinct curve above P fin	Membrane uniting D, C, and A fins well developed; Scales above nostrils shorter than nostrils

with species-specific traits (Whitehead *et al.* 1986; Cohen *et al.* 1990; Lloris *et al.* 2005; Froese & Pauly 2022). Interestingly, one of the two dab specimens exhibited left-side eye dominance (Figure 2).

#### Molecular study

The molecular study confirmed the initial assignment of fish taxa based on morphological features in all cases. Regardless of the barcoding marker used, the majority of the obtained sequences were 100% identical to publicly available records, and

some sequences were deposited in GenBank (Table 7). Sequences obtained for two species recorded in the PB, namely *M. merluccius* and *C. lucerna*, were submitted to GenBank under accession numbers OM737733 and OM737734, respectively. The most closely related records were those reported for *M. merluccius* (98.5%) and *C. lucerna* (99.8%), both from the North Sea. The *rho* nucleotide sequence of *S. rhombus* from our study matched that of a specimen collected from the PB in 2014 (Więcaszek *et al.* 2019). Additionally, the sequence was highly similar

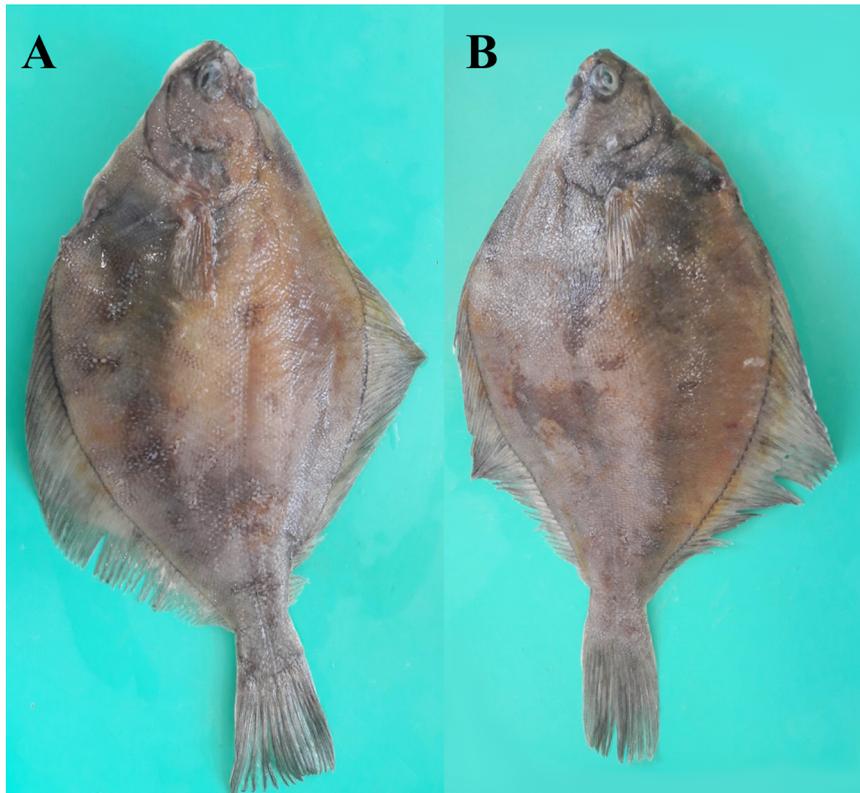


Fig. 2. Left-eye (A) and right-eye (B) specimens of *L. limanda* from the Pomeranian Bay.

Table 7

Results of the taxonomy confirmation via BLAST search against the NCBI Nucleotide Database

Sample ID	Species name	Molecular marker	Most similar sequence GenBank Acc. No. (sampling site)
Mer.mer.01	<i>M. merlangus</i>	<i>COI</i>	KJ205019 (North Sea)
Pol.vir.01	<i>P. virens</i>	<i>COI</i>	MK011284 (Norwegian Sea)
Mer.merluccius.01	<i>M. merluccius</i>	<i>rho</i>	OM737733 (Baltic Sea) <sup>1</sup> / FR832598 (North Sea)
Che.luc.01	<i>C. lucerna</i>	<i>cytb</i>	EU492097 (North Sea)
Che.luc.02	<i>C. lucerna</i>	<i>cytb</i>	OM737734 (Baltic Sea) <sup>1</sup> / EU492097 (North Sea)
Che.luc.03	<i>C. lucerna</i>	<i>cytb</i>	EU492097 (North Sea)
Che.luc.04	<i>C. lucerna</i>	<i>cytb</i>	EU492097 (North Sea)
Che.luc.05	<i>C. lucerna</i>	<i>cytb</i>	EF427548 (Cantabrian Sea)
Mul.sur.01	<i>M. surmuletus</i>	<i>rho</i>	EU637982.1 (France)
Mul.sur.02	<i>M. surmuletus</i>	<i>rho</i>	EU637982.1 (France)
Sco.sco.01	<i>S. scombrus</i>	<i>COI</i>	KX782690 (North Sea)
Sco.sco.02	<i>S. scombrus</i>	<i>COI</i>	KX782690 (North Sea)
Sco.sco.03	<i>S. scombrus</i>	<i>COI</i>	KX782690 (North Sea)
Sco.rho.01	<i>S. rhombus</i>	<i>rho</i>	KX980422 (Baltic Sea) / EU638005.1 (France) <sup>2</sup>
Sco.rho.02	<i>S. rhombus</i>	<i>rho</i>	KX980422 (Baltic Sea) / EU638005.1 (France) <sup>2</sup>
Lim.lim.01	<i>L. limanda</i>	<i>COI</i>	JN312159 (North Sea)
Lim.lim.02	<i>L. limanda</i>	<i>COI</i>	JN312159 (North Sea)
Sol.sol.01	<i>S. solea</i>	<i>rho</i>	EF439168 (Cantabrian Sea)
Sol.sol.02	<i>S. solea</i>	<i>rho</i>	EF439168 (Cantabrian Sea)

Note: Sequences reported were identical in pairwise comparisons to those listed in the last column. <sup>1</sup>Sequences were submitted to GenBank; <sup>2</sup>No sampling site information in GenBank; abbreviations: *COI* – cytochrome oxidase subunit I, *rho* – rhodopsin, *cytb* – cytochrome b.

(99.8%) to that of a fish most likely caught off the coast of France. Overall, the majority of sequences obtained in our study were identical to those of fishes inhabiting the North Sea, indicating spatial and temporal connections between the two seas.

## Discussion

The Baltic Sea offers a classic example of how an environmental gradient is linked to the distribution of marine species. However, there is limited knowledge regarding the origin of nonindigenous fishes in the Baltic. The presence of these fishes is likely attributed to inflows of saline water from the North Sea or rising sea temperatures (Matthäus *et al.* 2008).

In the present study, nine fish species were identified. European hake, common sole, and dab were observed for the first time in the PB, with the noteworthy discovery of a left-side-eyed specimen of dab. Additionally, whiting, tub gurnard, surmullet, Atlantic mackerel, and brill were infrequently recorded in this area. Saithe had been previously noted in the PB but not in the Szczecin Lagoon. The taxonomic identities of the collected specimens were successfully confirmed through morphometric and genetic analyses, and new barcodes were documented. The sequences obtained in this study showed a high degree of similarity with those of fishes inhabiting the North Sea, including one specimen of whiting, four specimens of tub gurnard, three specimens of mackerel, and two specimens of dab. The sequences of one tub gurnard specimen and two sole specimens were identical to data from the Cantabrian Sea (ICES Division VIIIc), while those of surmullet and dab matched data from the coasts of France (EU637982.1 and EU638005.1, respectively). The saithe sequence was identical to data from the Norwegian Sea. The new sequences of hake and tub gurnard were most similar to data from the North Sea.

The eastern boundary of the distribution for all examined species is Kattegat-Skagerrak, except for sole (ICES Division III SD 20-24), dab, and brill (SD 22-32) (ICES 2015; 2020; 2022). However, data from the available literature suggest a very rare occurrence of these species in the Baltic Sea. As per Heessen *et al.* (2015), sole, a southern species commonly found in the Kattegat (salinity > 25), is seldom encountered in the Baltic and is becoming increasingly scarce farther south and northeast. Sole exhibits a distinct genetic break between populations from the North Sea-Baltic Sea transition zone and the rest of the Atlantic Ocean. Cuveliers *et al.* (2012) demonstrated isolation-by-distance among sole pop-

ulations through microsatellite genotyping, identifying at least three different populations, namely, the Kattegat-Skagerrak region (ICES Division IIIa), the North Sea (Division IV), and the Bay of Biscay (Divisions VIII a,b).

Dab currently resides in the Kattegat and the western Baltic, whereas in the past, it was found in the central Baltic. The stock experienced a collapse after the Second World War and never recovered due to unfavorable hydrographic conditions (specifically, salinity requirements for egg development and the neutral buoyancy of eggs) and predation by cod (Temming 1989; Nissling *et al.* 2002; Ojaveer *et al.* 2010). Dab landings are primarily in SD 22, with smaller proportions in SD 24W. In SD 26-32, single specimens are caught only occasionally (ICES 2015).

According to Heessen *et al.* (2015), brill is regularly observed off Cape Arkona and around Bornholm; however, in the period of 2012-2016, landings were nonexistent in SD 24-32. The presence of brill specimens in the PB could result from either active migration from these areas or passive translocation with inflows of waters from the western Baltic. The initial record of brill in the PB was in 2014 (Więcaszek *et al.* 2019) and may be linked to a weak Major Baltic inflow (MBI) from the North Sea in March 2014, or possibly to two smaller inflow events in November 2013 and February 2014 (Naumann *et al.* 2017b).

Distinct groups of fish species can be delineated from the data obtained in our study and the literature on the PB. The first group comprises occasional marine visitors that seasonally migrate from the open Northeast Atlantic, the North Sea, and the Kattegat to the Baltic. However, they are unable to establish self-sustaining populations in the Baltic due to unfavorable environmental factors, such as excessively low salinity levels for reproduction (Ojaveer *et al.* 2010). An example of this is the tub gurnard, which is sporadically distributed in the western Baltic Sea. The second example is the mackerel, a species with long migratory patterns, where migration to and from the Baltic is influenced in part by climatic variables, including temperature. Mackerel is regularly found only in the southern Baltic and the Kattegat but spawns outside the Baltic Sea (HELCOM 2021). All specimens in our study were notably large, measuring 50 cm TL (pers. comm. fishers reported fish of 60 cm TL). According to Heessen *et al.* (2015), mackerel individuals longer than 22 cm were observed in the western half of the Baltic Sea but not in the PB. Other marine fish species from the North Sea that periodically migrate into the Baltic Sea include

whiting, saithe, seabass (*Dicentrarchus labrax*), European anchovy (*Engraulis encrasicolus*), grey mullets (*Chelon ramada* and *Chelon labrosus*), or swordfish (*Xiphias gladius*) (Krzykawski *et al.* 2001).

A second group of fish species is anticipated to expand its distribution northward in response to climate warming, and this includes surmullet (Engelhard *et al.* 2011). Beare *et al.* (2005) noted an increased abundance of this species in the northern North Sea, while Uiblein (2007) reported isolated occurrences in the Norwegian Sea. Ehrich *et al.* (2006) documented its presence in German waters. According to Więcaszek (2011), the region of its distribution encompasses the Skagerrak, the Kattegat, and the western Baltic, with the Kattegat stock residing at the edge of its distribution area, making it vulnerable. It cannot be ruled out that the thicklip mullet (*C. labrosus*) belongs to this group of fish, with its expansion from the southern North Sea toward the southwestern Baltic Sea potentially linked to increased sea temperatures as a consequence of climate change (Piatkowski & Schaber 2007). The occurrence of this species in the Baltic Sea was documented in the works of Więcaszek *et al.* (2011), Czerniejewski *et al.* (2008), and Schaber (2011). The thicklip mullet is euryhaline, displaying tolerance to a broad range of salinities and capable of osmoregulating even at extremely high salinities (Hotos & Vlahos 1998), making its survival in the saline waters of PB and the River Odra estuary highly probable.

The third group of species typically comprises fish that overflow from the Kattegat and the Belt Sea, including European hake (Heessen *et al.* 2015). This boreal-subtropic, benthopelagic species is abundant in the northern North Sea, the Skagerrak, and the Kattegat but notably absent from all but the most western part of the Baltic Sea (Heessen *et al.* 2015). The deep-water shark *Etmopterus spinax* (Więcaszek *et al.* 2018), ballan wrasse *Labrus bergylta* (Keszka & Raczyński 2002), or greater weever *Trachinus draco* (Krzykawski *et al.* 2001) serve as additional examples.

Freshwater runoff and inflows of North Sea water through the Danish Straits regulate the salinity levels and biodiversity of the Baltic Sea (Vuorinen *et al.* 2015). MBIs have a positive impact on the species diversity of the Baltic Sea (Mohrholz *et al.* 2015). The results of the current study, along with data from the literature concerning the occurrence of very rare fish species in the PB and inflows of saline North Sea water into the Baltic, affirm the correlation between these events (Figure 1). Inflows of saline waters from the North Sea occur sporadically, primarily

during winter, happening at most a few times annually. Since 1887, the frequency and intensity of MBIs have not changed, despite noticeable multidecadal variability with a main period of 25-30 years. Although there is no clear trend in the frequency and intensity of MBIs on a decadal time scale, climate change appears to reduce the frequency of MBIs (Mohrholz 2018). MBIs in the winters of 1993-1994, 1997-1998, 2002-2003, and 2014-2015 were notably evident in the Gotland Basin. Beginning in 1998, the deep water became warmer than in the previous period (Raudsepp *et al.* 2018). Even moderate inflows, as observed in the winters of 1997-1998, 2006-2007, and 2018-2019, brought warmer water to the bottom layer of the Gotland Basin (Copernicus Marine Service 2021). The inflow during the winter of 2010-2011 was estimated to be weak (Naumann *et al.* 2017b).

The third-largest MBI, categorized as very strong, observed since 1880 occurred in December 2014, bringing substantial amounts of saline water into the Baltic Sea (Naumann *et al.* 2016; Liblik *et al.* 2017). This hydrological event may be significantly linked to a higher number of occurring nonindigenous fish species in the PB. This event followed a stagnation period of two decades since the very strong inflow in 1993-1994. The strength of the 2014-2015 MBI considerably surpassed that of 2002-2003 (Mohrholz *et al.* 2015). In November 2015, a series of 12 low-pressure cells crossed the Baltic Sea, and during the winter of 2015-2016, two MBIs of moderate intensity followed the previous ones. In September 2016, a baroclinic inflow was observed at the Darss Sill (Belt Sea) (Naumann *et al.* 2016). Most of the nonindigenous fish species (nine) were recorded after the 2014-2015 inflow. For example, European hake was noted in the PB in 2015, and in the same year, Bacevičius and Kregždys (2017) reported one specimen in the Baltic waters of Lithuania, marking the first documented report of this species in the brackish area of the southeastern Baltic Sea. The most spectacular newcomer to the PB was the deep-water shark, caught for the first time (and so far, only once) in the Baltic Proper in 2016, following either the MBI of 2014-2015 or that of winter 2015-2016 (Więcaszek *et al.* 2018).

Following the inflow in the winter of 1993-1994, two new fish species were observed in 1995 and 1996. Subsequently, after the inflow in the winter of 1996-1997, five species were recorded in 1998-2000. Following the inflow in the winter of 2006-2007, two new fish species were noted in 2007, and in 2010, the lumpfish *Cyclopterus lumpus* was reported. Although the lumpfish is considered a common species

in the PB, it appeared to originate from the North Sea due to its large size (over 40 cm TL), a characteristic not previously reported in the Baltic Sea (Więcaszek *et al.* 2015). After the inflow in the winter of 2010-2011, two new species were discovered, and subsequently, two extremely rare fish species were reported in 2011, 2013, and 2014. In the most recent period of examined inflows (2018-2019), three nonindigenous fish species were recorded, including a sole, which is extremely rare in the Baltic Proper (noted in 2017 and 2019), likely following the MBIs in 2016 and 2018-2019 (Figure 1). The first report of this species was in 2007 (in the waters of Lithuania), probably after the inflow in the winter of 2006-2007 (Bacevičius & Karalius 2008). It is worth noting that in the Red List of marine fish species of Germany, all recorded species, except hake, are listed as native species (Thiel *et al.* 2013).

Over the past 60 years in the Baltic Sea region, the duration of high sea levels has increased by one-third, the frequency of storm surges has risen (from 3.1 to 5.5 per year), and the maximum sea level has also been on the incline (0.28 cm per year). These changes are attributed to the intensification of western circulation and the overall rise in global mean sea level, both linked to processes associated with global warming (Wolski & Wiśniewski 2021). It is likely that such extreme weather conditions will result in an increased occurrence of rare fish species, making them suitable bioindicators of the changing environment.

## Conclusions

The presence of nonindigenous and rare fish species in the study area may result from inflows of saline water, periodic migrations of fish from the western Baltic, and the northward extension of the distribution of some species in response to climate warming, particularly during extreme weather conditions.

The findings of the present study indicate that analyzing bycatch involving rarely occurring and nonindigenous fish species in the PB can, to a certain extent, serve as a reflection of environmental changes in the area.

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## Author Contributions

Research concept and design B.W.; Collection and/or assembly of data: B.W., R.P., P.E., A.T., A.B.; Data analysis and interpretation: B.W., R.P., P.E.; Writing the article: B.W., R.P., P.E.; Critical revision of the article: B.W., R.P., P.E.; Final approval of article: B.W., R.P., P.E.

## Conflict of Interest

The author declares no conflict of interest.

## Supplementary Material

Supplementary Materials to this article can be found online at:

<http://www.isez.pan.krakow.pl/en/fovia-biologica.html>

Supplementary files:

SM.01. Molecular marker sequences of collected samples.

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