Abstract—Distribution patterns of larval flatfish assemblages at 3 oceanographic monitoring stations off southeastern Australia (North Stradbroke Island [NSI], about 27°30′S; Port Hacking [PH], about 34°6′S; and Maria Island [MAI], about 42°30′S) are described from monthly ichthyoplankton samples collected between 2014 and 2021. A total of 4873 flatfish larvae were collected from 6 families: Bothidae (*Arnoglossus* spp., intermediate flounder [*Asterorhombus intermedius*], *Crossorhombus* spp., *Engyprosopon* spp., *Grammatobothus* spp., and crested flounder [*Lophonectes gallus*]), Cynoglossidae, Paralichthyidae (*Pseudorhombus* spp.), Pleuronectidae, Samaridae, and Soleidae. Abundances of different taxa varied seasonally, and the assemblage composition varied between seasons and years, but with no overall change in abundances over the study period. Markedly different larval flatfish assemblages were caught at the 3 stations, corresponding to the latitudinal variation in water mass characteristics (temperature, salinity, and chlorophyll). The number of larval flatfish taxa decreased with increasing latitude and were highest at the sub-tropical NSI and lowest at the temperate MAI. Most bothid larvae were caught at NSI and PH except crested flounder, which was only caught at PH and MAI. Cynoglossid, *Pseudorhombus* spp., samarid, and soleid larvae were only caught at NSI and PH, while pleuronectid larvae were only caught at MAI. These distinct larval assemblages provide

Seasonal and oceanographic variation in larval flatfish assemblages off the southeast Australian coast

Anthony G. Miskiewicz (contact author)[1,4]
Indiana J. Riley[1,4]
Amelia J. Caley[1]
Paloma A. Matis[2,3]
Iain M. Suthers[1,2]

Email address for contact author: tonymisk@yahoo.com

[1] School of Biological, Earth and Environmental Science
    University of New South Wales
    Sydney, New South Wales 2052, Australia

[2] Sydney Institute of Marine Science
    19 Chowder Bay Road
    Mosman, New South Wales 2088, Australia

[3] School of Biological Science
    University of Sydney
    Sydney, New South Wales 2006, Australia

[4] Ichthyology
    Australian Museum Research Institute
   Sydney, New South Wales, 2010, Australia

Introduction

Most marine fish species have a planktonic larval stage, during which survival and dispersal determine juvenile recruitment and adult abundance (Horwood et al., 2000). The larval fish assemblage occurring in a study area depends not only on the diversity and abundance of adult fish spawning locations and strategies but also on the behavior of the developing larvae (Rodriguez, 2019). Ocean boundary currents and the presence of fronts and eddies also influence larval fish assemblage composition by accumulating or dispersing larvae away from the spawning area, as well as transporting larvae spawned elsewhere into the study region (Hare et al., 2001; Bakun, 2006; Garcia et al., 2022).

The dominant oceanographic feature off eastern Australia is the East Australian Current (EAC), a western boundary current that flows south from the Coral Sea poleward along the eastern Australian coast (Fig. 1) (Cetina-Heredia et al., 2014; Oke et al., 2019). A transition zone separating tropical and temperate systems occurs in the region between 30°S and 32°S, where the EAC separates from the coast and flows eastward into the

Tasman Sea (TAS) along the Tasman Front (Cetina-Heredia et al., 2014; Oke et al., 2019). The remainder of the current flows southward to form the EAC extension (Cresswell, 2000; Hill et al., 2008). The EAC exhibits seasonal and multi-decadal variability: strengthening in summer and weakening in winter (Roughan et al., 2011; Oke et al., 2019). There are various proposals as to the cause of this variability, but the mechanisms driving the separation of the EAC from the coast are not fully understood (Oke et al., 2019).

Adult fish diversity on the eastern Australian continental shelf decreases progressively from low to high latitudes (Last et al., 2011). The decrease in adult species diversity with increasing latitude is also reflected in the larval fish assemblages along the southeast coast of Australia (Keane and Neira, 2008; Hinchliffe et al., 2021). Further variation in larval assemblage composition is associated with bathymetry, the Tasman Front, and smaller oceanographic features such as eddies. One study found that the number of taxa decreases with distance offshore along the Tasman Front, and more taxa occurred in the warmer Tasman Front compared with
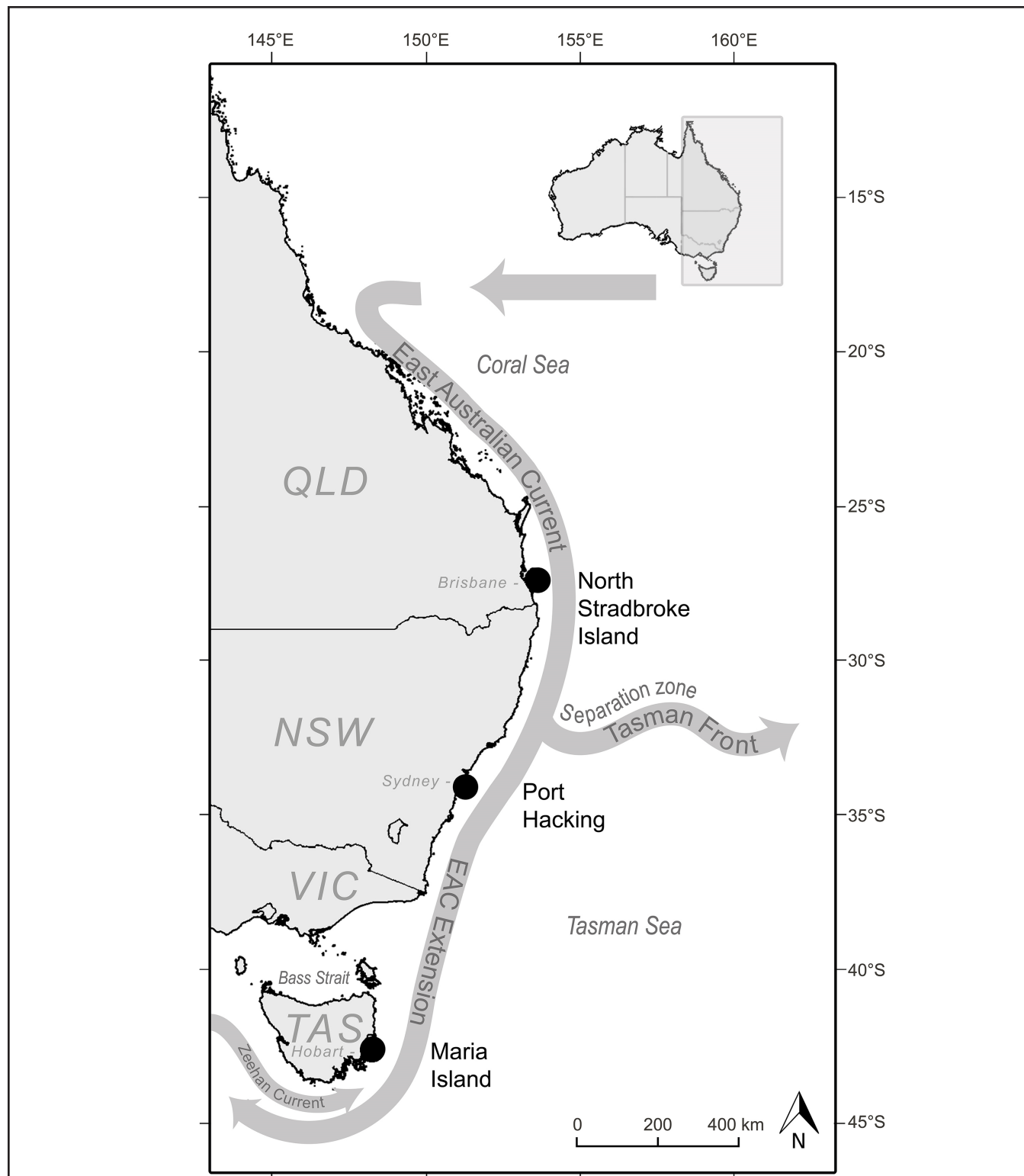
Figure 1

Map of eastern Australia showing the major ocean currents (arrows) and locations (dots) of the Integrated Marine Observing System National Reference Stations where ichthyoplankton samples were collected monthly during 2014–2021: North Stradbroke Island (Queensland [QLD]), Port Hacking (New South Wales [NSW]), and Maria Island (Tasmania [TAS]). VIC=Victoria.

the cooler TAS (Mullaney et al., 2011). There was a general trend of greater richness in larval fish families on the shelf compared with other bathymetric zones (slope and ocean) and slightly higher richness in a cyclonic than in an anticyclonic eddy (Matis et al., 2014). The southeast of Australia is a climate change hot spot with the EAC warming and strengthening at a rapid rate in comparison to other regions of the world (Wu et al., 2012; Oke et al., 2019; Malan et al., 2021), which is facilitating tropicalization of temperate systems (Johnson et al., 2011; Vergés et al., 2014). Long-term larval fish monitoring programs, such as the Integrated Marine Observing System (IMOS) larval fish monitoring program, provide a basis for assessing the current composition of larval fish assemblages along the coast and for monitoring changes in these assemblages over time (Hinchliffe et al., 2021), such as those driven by tropicalization (Smith et al.[1]; Lara-Lopez et al.[2]).

Larval flatfishes of the order Pleuronectiformes are a useful taxonomic group to assess spatial and temporal changes in larval fish assemblages due to their distinct morphology, widespread distributions, high abundances, and association with different water masses (Bailey and Picquelle, 2002; Bailey et al., 2005, 2008). Flatfishes are distributed throughout most oceans from the Arctic (80°S) to about 60°S (Pauly, 1994). The highest diversity of flatfishes occurs in tropical waters, although characterized by limited biomass and fisheries. They support large-scale fisheries in northern hemisphere temperate and boreal waters, with only small fisheries occurring in southern hemisphere waters (Pauly, 1994). Along the eastern Australian coast, adult flatfish diversity is highest in warmer tropical waters, and diversity decreases towards cooler temperate waters at higher latitudes. Seven flatfish families comprising 29 genera and more than 50 species are recorded off Brisbane (27°18′S); 5 families, 18 genera, and 26 species off Sydney (34°6′S); and 2 families, 6 genera and 8 species off Hobart (42°36′S) (FISHMAP, available from http://www.marine.csiro.au/data/caab/fishmap.cfm, accessed August 2022) (Rees et al., 2022).

Compared with regions such as the North Sea and the Gulf of Alaska (Bailey and Picquelle, 2002; Bailey et al., 2005, 2008), there is very limited species-specific in-

formation on adult spawning strategies and assemblage and distribution patterns of flatfish larvae in relation to oceanography in southeast Australian waters. Information for identifying temperate Australian species is limited, with few published descriptions of larval flatfish developmental series (Liew, 1983; Crawford, 1986; Liew, 1986; Liew et al., 1988; Fukui et al., 2002). Although flatfish larvae are frequently observed in ichthyoplankton surveys in southeast Australian waters (Smith et al., 2018), only crested flounder (*Lophonectes gallus*) larvae have been identified to species (Fukui et al., 2002; Keane and Neira, 2008). Flatfish larvae were only reported to family level for other surveys in the region (Gray and Miskiewicz, 2000; Mullaney et al., 2011; Mullaney and Suthers, 2013; Matis et al., 2014; Garcia et al., 2022). Compared with previous studies, the identification of larvae from the family Bothidae to genus or species in this study improves our understanding of taxa-specific spawning locations, seasonality, and differences in larval assemblages in different water masses along the southeast coast of Australia.

Flatfish larvae were categorized based on their adult distributions (Liew, 1983; Gomon et al., 2008; FISHMAP, Rees et al., 2022). Tropical taxa include the families Bothidae (intermediate flounder [*Asterorhombus intermedius*], *Crossorhombus* spp., *Engyprosopon* spp., and *Grammatobothus* spp.) and Samaridae. Tropical and temperate taxa include families Bothidae (*Arnoglossus* spp.), Paralichthyidae (*Pseudorhombus* spp.), Cynoglossidae, and Soleidae. Representatives of these taxa have a widespread distribution around northern Australia and across the broader Indo-Pacific region. In contrast, the temperate bothid crested flounder is endemic to the shallow coastal waters of southeast Australia and New Zealand (Fukui et al., 2002; Gomon et al., 2008). Taxa in the family Pleuronectidae also have a restricted distribution around southern Australia and New Zealand (Gomon et al., 2008).

This study aims to describe the spatial, interannual, and seasonal distribution patterns in the larval flatfish assemblages based on samples collected at 3 long-term monitoring locations in the southeast Australian region. The specific aims of this study were to 1) provide a latitudinal comparison of the number of taxa and their abundances in the larval flatfish assemblage, 2) identify seasonal and interannual trends in larval flatfish assemblages, and 3) assess the differences in distributions of larval flatfish taxa within the different water masses along the southeast Australian coast. Based on the pattern of decreasing diversity with latitude of adult flatfish species, we hypothesize that the number of larval flatfish taxa would decrease with increasing latitude and that the larvae of tropical taxa would only occur in higher latitude waters during warmer seasons of the year. With the predicted warming and strengthening of the EAC, it

[1]Smith, J. A., I. M. Suthers, A. Lara-Lopez, A. Richardson, K. M. Swadling, T. Ward, P. Van Ruth, and J. Everett. 2016. An evaluation of plankton monitoring at IMOS national reference stations. Final report to the Australian Fisheries Management Authority, Proj. 2015/0819, 67 p. [Available from https://www.afma.gov.au/research/evaluation-ichthyoplankton-monitoring-imos-national-reference-stations.]

[2]Lara-Lopez, A., C. Hinchliffe, I. M. Suthers, A. J. Richardson, and P. A. Matis. 2020. Temporal and spatial changes in larval fish. In State and trends of Australia's ocean report (A. J. Richardson, R. Eriksen, T. Moltmann, I. Hodgson-Johnston, and J. R. Wallis, eds.), 3 p., Integrated Marine Observing System, Hobart, Australia. [Available from https://doi.org/10.26198/5e16b12149e8b.]

is expected that in the future, tropical flatfish larvae will be more abundant and extend their distribution further south into temperate waters (Johnson et al., 2011; Vergés et al., 2014).

Materials and methods

Study area

Sampling was carried out at 3 IMOS National Reference Stations (NRSs) located along the southeast coast of Australia as part of the IMOS larval fish monitoring program (Smith et al.[1]; Lara-Lopez et al.[2]). Samples were collected at North Stradbroke Island, Queensland (27.3°S, 153.6°E), Port Hacking, New South Wales (34.1°S, 151.2°E), and Maria Island, Tasmania (42.6°S, 148.2°E) (Fig. 1). The 3 NRSs span approximately 15° of latitude at roughly equidistant points along the east coast of Australia, and different oceanographic conditions characterize each NRS. The EAC dominates North Stradbroke Island and represents an important biogeographic boundary point between tropical and temperate waters. Between 30°S and 32°S, most of the EAC separates from the coast to form the eastward-flowing Tasman Front (Hill et al., 2008). Port Hacking, located south of the separation zone, is influenced by the southward-flowing EAC extension and associated cyclonic and anti-cyclonic eddies. Maria Island is influenced by the seasonal extension and retraction of the southward flowing EAC extension and the Zeehan Current flowing eastward from the Great Australian Bight (Cresswell, 2000).

Ichthyoplankton collection

Larval fish sampling was conducted approximately monthly from 2014 through 2021 at 2 locations, separated by <1 km, at each of the 3 NRSs following methods detailed in Davies and Sommerville (2020). From 2014 through 2019, tows were conducted using either a single 75×75-cm[2] net or an 85-cm diameter ring net with 500-μm mesh. From early 2019 onwards, nets were changed to a 60-cm diameter bongo net with 500-μm mesh across all stations. The overall mouth area of both net types was the same, and for each sample, larval counts were standardized by tow volume to convert larval concentrations per 100 m[3]. Nets were deployed to approximately 25 m depth, gradually towed obliquely to 5 m depth below the surface, and then retrieved. The net was towed at 1.5 m/s (about 3 knots through the water) over a period of 12 min. A HOBO depth logger (Onset Computer Corp., Bourne, MA) recorded the depth of each tow, and tow volume was recorded using a flowmeter attached across the mouth of the net. Differences in net type and flowmeters (2030R flowmeter, General Oceanics, Miami, FL and Tsurumi-Seiki flowmeter, Tsu-

rumi-Seiki Co., Yokohama, Japan) accounted for when calculating the volume of water sampled. Prior to 2016, both samples at North Stradbroke Island and Port Hacking and prior to 2018 at Maria Island were fixed in 4% neutral buffered formalin. Subsequently, one square net sample or one net of each bongo tow was immediately preserved in either 95% ethanol (drained and refilled after 1 to 3 days) and the other sample in formalin.

All larval fish were sorted from each sample into individual vials using a stereo light microscope (TLI-MS6 stereo zoom, The Logical Interface, Illawong, New South Wales, Australia). After sorting from the bulk sample, larvae from ethanol-fixed samples were transferred to 80% ethanol and stored at –20°C for future cytochrome c oxidase 1 barcoding, and larvae from formalin-fixed samples were transferred to 70% ethanol. For each bongo net tow, both samples were initially sorted, identified, and stored separately, and the data for both nets were then combined to give a total abundance for each sample. Larval flatfishes in the samples were identified to the lowest possible taxon using available literature (Liew, 1983; Crawford, 1986; Liew, 1986; Ozawa and Fukui, 1986; Fukui et al., 2002; Okiyama, 2014). A total of 11 flatfish taxonomic groups were identified in the samples with the possible number of species for each taxon in brackets: Bothidae (*Arnoglossus* spp. [7 species]), intermediate flounder, *Crossorhombus* spp. [2 species], *Engyprosopon* spp. [5 species], *Grammatobothus* spp. [2 species], crested flounder, Cynoglossidae (2 genera and 4 species), Paralichthyidae (*Pseudorhombus* spp. [6 species]), Pleuronectidae (2 genera and 4 species), Samaridae (3 genera and 3 species), and Soleidae (15 species).

Statistical analysis

We standardized counts by total tow volume, converting them to larval concentrations per 100 m[3], to compare larval fish counts across different net types and NRSs. Larval fish concentrations were then log-transformed ($\log_{10}+1$) to reduce the influence of taxa with very large abundances and increase the influence of rare taxa on the larval assemblages. Differences in larval concentrations between NRSs and seasons and within NRSs over time were then visualized using box plots and line graphs.

All statistical analyses were performed using R, vers. 4.0.4 (R Core Team, 2021). Multivariate generalized linear models (MGLMs) using the manyglm function from the mvabund package (Wang et al., 2012) were computed for the larval abundance data to determine differences in larval assemblages between NRSs, seasons, and years. The MGLMs using mvabund were chosen over other distance-based analyses as they are designed specifically for use with abundance datasets, including an assumed mean-variance relationship and improved power for a range of taxa with different variances (Wang et al.,

2012), and have been used in other studies of larval fish assemblages (Hinchliffe et al., 2021; Garcia et al., 2022). For all MGLM analyses, raw abundance was used as the response variable, $\log_{10}$ (sampling volume in cubic meters) was used as an offset, and models had a negative binomial error distribution.

To test whether taxa composition differed between NRSs and determine which taxa were driving any differences, generalized linear models (GLMs) were fitted to each taxa using the following formula:

$$mod1 <-manyglm(Flatfish\_taxa$$
$$Data\$NRS\_Name, family="negative\_binomial",$$
$$offset=log(Data\$Volume\_m3)), \qquad (1)$$

where *mod1*=the GLM output;

> *manyglm*=the function used to fit the GLM;
>
> *Flatfish_taxa*=the response variable abundance (an *mvabund* object containing the abundance data for all flatfish taxonomic groups);
>
> *Data$NRS_Name*=the predictor variable site (the 3 NRSs);
>
> *family = negative_binomial*=the mean-variance relationship specified between our data (negative binomial); and
>
> *offset = log(Data$Volume_m3)*=offsetting a predictor variable ($\log_{10}$ sampling volume) known to be proportional to the response variable (abundance).

Univariate *taxa-by-taxa* adjusted *P* values were then calculated using the *p.uni* argument in the mvabund package.

To test whether the assemblage composition differed across NRSs, seasons, and years, and whether there were any interactions between these factors, GLMs were fitted to each taxa using the following formula:

$$mod2 <-manyglm(Flatfish\_taxa \sim Data\$NRS$$
$$Name*Data\$Season*Data\$Year, family="negative$$
$$binomial", offset=log(Data\$Volume\_m3)), \qquad (2)$$

where *mod2*=the GLM output; and

> *DataNRS_DataNRS_Name*Data$Season *Data$Year*=the predictor variables' site (the 3 NRSs), season, and year respectively.

Finally, this test was repeated with temperature, salinity, and chlorophyll as fixed factors to test the impacts of these physical parameters on the assemblages at the 3 NRSs using the following formula:

$$mod3 <-manyglm(Flatfish\_taxa \sim Data\$$$
$$Temperature+Data\$Salinity+Data\$Chlorophyll,$$
$$family="negative\_binomial", offset=log$$
$$(Data\$Volume\_m3)), \qquad (3)$$

where *mod3*=the GLM output; and

> *Data$Temperature+Data$Salinity+Data$Chlorophyll*=the predictor variables temperature, salinity, and chlorophyll respectively.

To visualize the differences in larval assemblages across NRSs, seasons, and different levels of environmental parameters, an unconstrained Gaussian copula latent variable ordination was created using ecoCopula, vers. 1.0.1 (Popovic et al., 2019) from the MGLM intercept-only model using the following formula:

$$mod\_null <-manyglm(Flatfish\_taxa \sim 1,$$
$$family="negative\_binomial", offset=log$$
$$(Data\$Volume\_m3)), \qquad (4)$$

where *mod_null*=the GLM output.

Gaussian copula latent variable ordination was chosen over distance-based ordination methods, as like the MGLM analysis chosen above, they allow for the assumption of a mean-variance relationship between data points by using count data directly (Popovic et al., 2019), and GLM ordination using a combination of the mvabund and ecoCopula packages has been used in other larval assemblage studies (Hinchliffe et al., 2021). Finally, larval concentrations of the different flatfish taxa were plotted against the water temperature and salinity corresponding to each larval sample to visualize their variation in abundance against these physical parameters at the 3 NRSs.

Time series graphs were created to initially visualize the differences in temperature, salinity, and chlorophyll over time between the 3 NRSs. To determine which physical variables differed the most between the NRSs, principal component (PC) analysis was run on the log-transformed physical parameters using the princomp function from the stats package (R Core Team, 2021). Analysis was based on a correlation matrix, with all variables scaled to ensure unit variance.

Physical oceanographic data

At each NRS, data for both physical and biogeochemical variables were collected at approximately monthly intervals to characterize the ocean environment and to understand biological processes within the water column (available through the Australian Ocean Data Network Portal, https://portal.aodn.org.au/, accessed July 2022). A Seabird 19plus V2 Seacat Profiler (Sea-Bird Scientific, Bellevue, WA) was used for vertical profiling measurements of conductivity (salinity), temperature, depth, oxygen, fluorometry, and turbidity. Niskin bottle samples (model 1010, General Oceanics) at discrete 10-m intervals were taken to measure dissolved inorganic carbon, alkalinity, and nutrients. Larval fish sampling was

conducted in conjunction with the water sampling at each NRS. For each sampling event, temperature, salinity, and chlorophyll measurements were averaged for the top 30 m of the water column and matched with the larval flatfish concentrations in the corresponding samples. Oceanographic data were grouped into 3-month intervals based upon monthly average water temperatures as follows: spring (September–November), summer (December–February), autumn (March–May), and winter (June–August).

Results

Flatfish larvae assemblages

Over the 8 years of sampling at the 3 NRSs, a total of 4873 flatfish larvae from 11 taxa were collected (Table 1). Overall, patterns of flatfish abundance and number of taxa differed across NRSs and seasons within NRSs (Fig. 2, Suppl. Figs. 1 and 2). The highest abundance of flatfish larvae was recorded at North Stradbroke Island, with 9 taxa comprising 2578 larvae. At Port Hacking, 8 taxa comprising 1492 larvae were recorded, and at Maria Island, 3 taxa comprising 803 larvae were recorded (Table 1). Four bothid taxa (intermediate flounder, *Crossorhombus* spp., *Engyprosopon* spp., and *Grammatobothus* spp.) were recorded at North Stradbroke Island and Port Hacking. Crested flounder was only caught at Port Hacking and Maria Island, while *Arnoglossus* spp. was caught at all 3 stations (Fig. 3). *Pseudorhombus* spp., cynoglossid, samarid, and soleid larvae were only caught at North Stradbroke Island and Port Hacking, while pleuronectid larvae were only caught at Maria Island (Fig. 2).
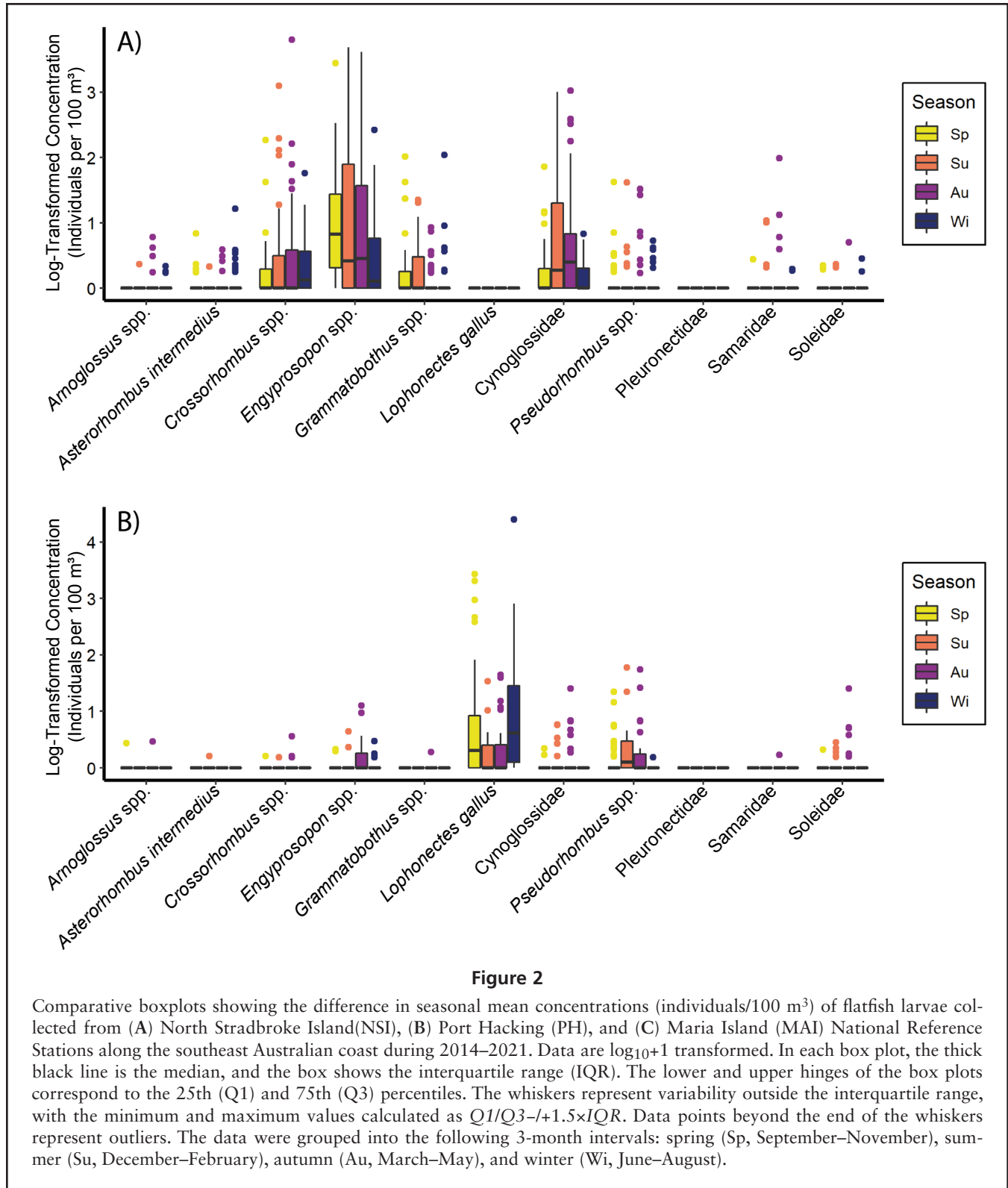
At North Stradbroke Island, the most abundant taxa were 5 genera from Bothidae. The most abundant taxon was *Engyprosopon* spp. (55.4%), followed by *Crossorhombus* spp. (14.6%) and *Grammatobothus* spp. (5.9%) (Fig. 2A). Other abundant taxa included cynoglossids (18.5%) and *Pseudorhombus* spp. (2.8%), while lower abundances included samarids (1.2%) and soleids (0.4%). At Port Hacking, 5 genera of Bothidae made up the highest abundances, with crested flounder (82.8%) as the most abundant (Fig. 2B). Other abundant taxa included *Pseudorhombus* spp. (8.6%) and cynoglossids (3.0%), while soleids (2.2%) were the least abundant. At Maria Island, 2 genera from Bothidae were the most abundant taxa, with crested flounder (86.4%) as the dominant taxon, and there were lower abundances of pleuronectids (13.5%) (Fig. 2C).
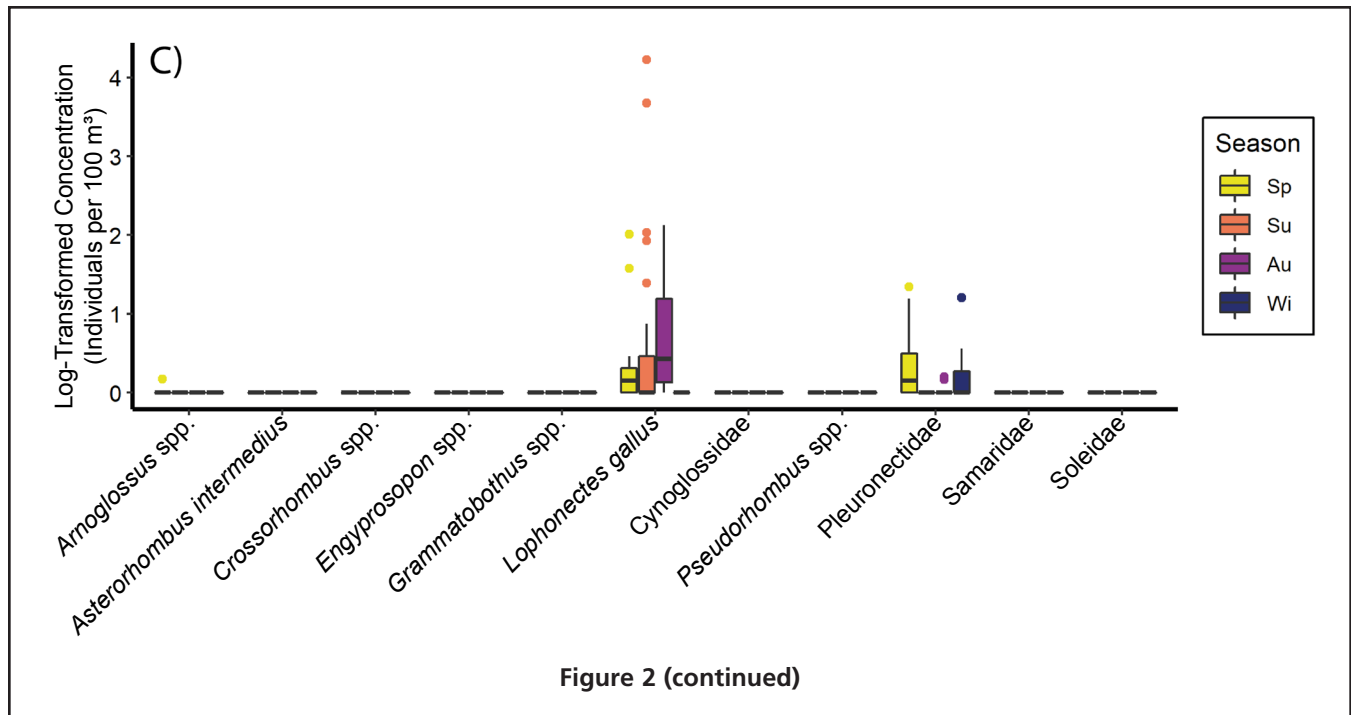
The GLM results showed that the flatfish larval assemblage composition was significantly different (*P*<0.05) between the 3 NRSs (deviance [Dev]=786.4, *P*<0.001), seasons (Dev=242.4, *P*<0.001), and years

Table 1

Overall abundances (raw counts) and minimum (min), maximum (max), mean, and standard deviation (SD) concentrations (conc; individuals/100 m3) of larval flatfish collected monthly at North Stradbroke Island, Port Hacking, and Maria Island National Reference Stations (NRS) along the southeast Australian coast during 2014–2021.

Species	North Stradbroke Island NRS					Port Hacking NRS					Maria Island NRS				
	Overall abundance	Min conc	Max conc	Mean conc	SD	Overall abundance	Min conc	Max conc	Mean conc	SD	Overall abundance	Min conc	Max conc	Mean conc	SD
Arnoglossus spp.	11	0.00	1.18	0.03	0.13	3	0.00	0.59	0.01	0.06	1	0.00	0.19	0.00	0.02
Asterorhombus intermedius	31	0.00	2.37	0.06	0.24	1	0.00	0.23	0.00	0.02	0	0.00	0.00	0.00	0.00
Crossorhombus spp.	382	0.00	43.79	0.99	3.88	6	0.00	0.74	0.01	0.07	0	0.00	0.00	0.00	0.00
Engyprosopon spp.	1434	0.00	38.89	3.44	7.19	36	0.00	2.02	0.07	0.25	0	0.00	0.00	0.00	0.00
Grammatobothus spp.	126	0.00	6.69	0.30	0.88	1	0.00	0.32	0.00	0.03	0	0.00	0.00	0.00	0.00
Lophonectes gallus	0	0.00	0.00	0.00	0.00	1236	0.00	80.28	2.33	7.66	694	0.00	67.37	1.53	7.15
Bothidae other	0	0.00	0.00	0.00	0.00	3	0.00	0.45	0.01	0.05	2	0.00	0.21	0.00	0.03
Cynoglossidae	478	0.00	19.53	1.19	3.02	44	0.00	3.06	0.08	0.33	0	0.00	0.00	0.00	0.00
Pseudorhombus spp.	74	0.00	4.07	0.19	0.64	128	0.00	4.90	0.25	0.73	0	0.00	0.00	0.00	0.00
Pleuronectidae	0	0.00	0.00	0.00	0.00	0	0.00	0.00	0.00	0.00	108	0.00	2.84	0.18	0.48
Samaridae	31	0.00	6.29	0.09	0.54	1	0.00	0.26	0.00	0.02	0	0.00	0.00	0.00	0.00
Soleidae	11	0.00	1.01	0.02	0.11	33	0.00	3.06	0.06	0.29	0	0.00	0.00	0.00	0.00

Figure 2

Comparative boxplots showing the difference in seasonal mean concentrations (individuals/100 m³) of flatfish larvae collected from (**A**) North Stradbroke Island(NSI), (**B**) Port Hacking (PH), and (**C**) Maria Island (MAI) National Reference Stations along the southeast Australian coast during 2014–2021. Data are $\log_{10}+1$ transformed. In each box plot, the thick black line is the median, and the box shows the interquartile range (IQR). The lower and upper hinges of the box plots correspond to the 25th (Q1) and 75th (Q3) percentiles. The whiskers represent variability outside the interquartile range, with the minimum and maximum values calculated as $Q1/Q3-/+1.5\times IQR$. Data points beyond the end of the whiskers represent outliers. The data were grouped into the following 3-month intervals: spring (Sp, September–November), summer (Su, December–February), autumn (Au, March–May), and winter (Wi, June–August).

Figure 2 (continued)

(Dev=56.4, *P*<0.001) (Suppl. Table 1). Univariate post-hoc testing showed that all flatfish taxa differed significantly between the 3 NRSs (*P*<0.001, Suppl. Table 1), except for *Arnoglossus* spp. (Dev=2.4, *P*=0.427) and *other* bothid group (Dev=3.5, *P*=0.427) (Suppl. Table 1). Gaussian ordination of the flatfish larvae data for the 3 NRSs combined over time showed a clear separation among assemblage groups (Fig. 3). Latent variable 1 showed a clear separation of the assemblage at North Stradbroke Island from Port Hacking and Maria Island. North Stradbroke Island was characterized by the tropical bothids intermediate flounder, *Crossorhombus* spp., *Engyprosopon* spp., and *Grammatobothus* spp., and by cynoglossids and samarids. The Port Hacking and Maria Island assemblages were dominated by crested flounder at both NRSs, and pleuronectids were only caught at Maria Island. On latent variable 2, the North Stradbroke Island and Port Hacking assemblages were clearly separated from Maria Island based on concentrations of *Pseudorhombus* spp.

Seasonal trends in larval flatfish abundances

At North Stradbroke Island, flatfish larvae were caught in all seasons, with the highest abundances during summer and the lowest in winter. At Port Hacking, larvae were caught in all seasons. Crested flounder, the dominant taxon, had the highest abundance at this station during winter through spring and lower abundances during summer through autumn. For other taxa, the highest larval abundances occurred during summer through au-
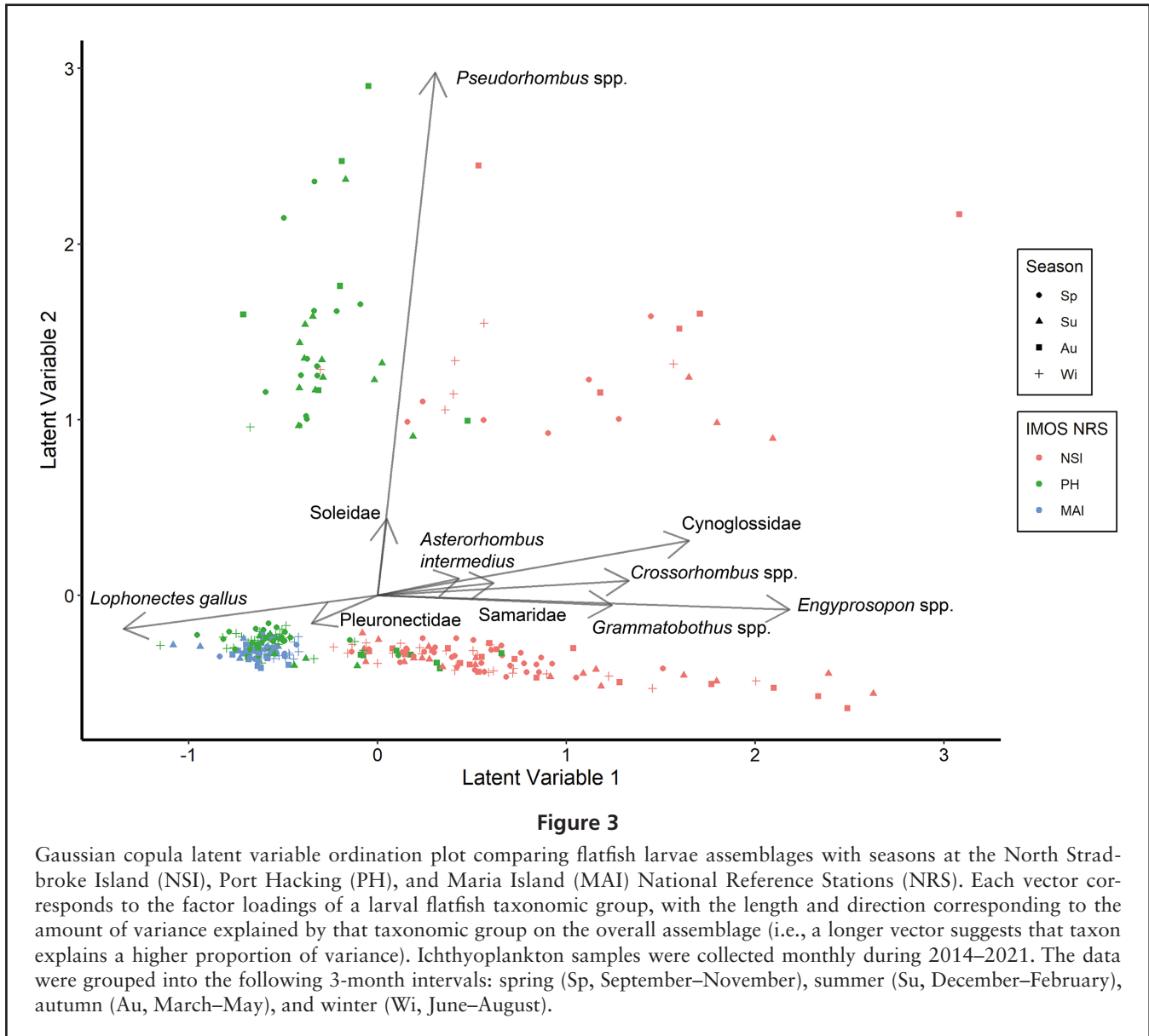
tumn and were lowest in winter. At Maria Island, larvae were caught in all seasons, with the highest abundance of crested flounder during autumn and the lowest abundance in winter. For pleuronectids, the highest abundances occurred during winter through spring, and none were caught in summer.

There were significant interactions between NRSs and seasons (Dev=136.9, *P*<0.001) and NRSs and years (Dev=57.2, *P*<0.001) (Suppl. Table 2), suggesting that within each NRS, larval flatfish assemblage composition changed between seasons and years. There were no significant interactions between seasons and years (Dev=46.2, *P*=0.074) or between NRSs, seasons, and years (Dev=9.8, *P*=0.761) (Suppl. Table 2), suggesting that spatial and seasonal patterns in larval flatfish assemblages were stable throughout the 8-year study period.

General oceanographic conditions

There was a clear trend of decreasing water temperatures towards southern latitudes and a seasonal pattern at each NRS (Fig. 4). The highest mean water temperature was recorded at North Stradbroke Island, 23.5°C (range: 20.1–27.6°C), followed by a mean of 19.8°C (range: 15.8–26.0°C) at Port Hacking, and a mean of 14.6°C (range: 11.8–19.6°C) at Maria Island. Salinities were variable at the 3 NRSs, with the salinity at Maria Island generally lower compared with North Stradbroke and Port Hacking (Suppl. Fig. 3). The low salinity value recorded at Port Hacking in February 2020 was due to an extreme rainfall event. Sensors at Port Hacking con-
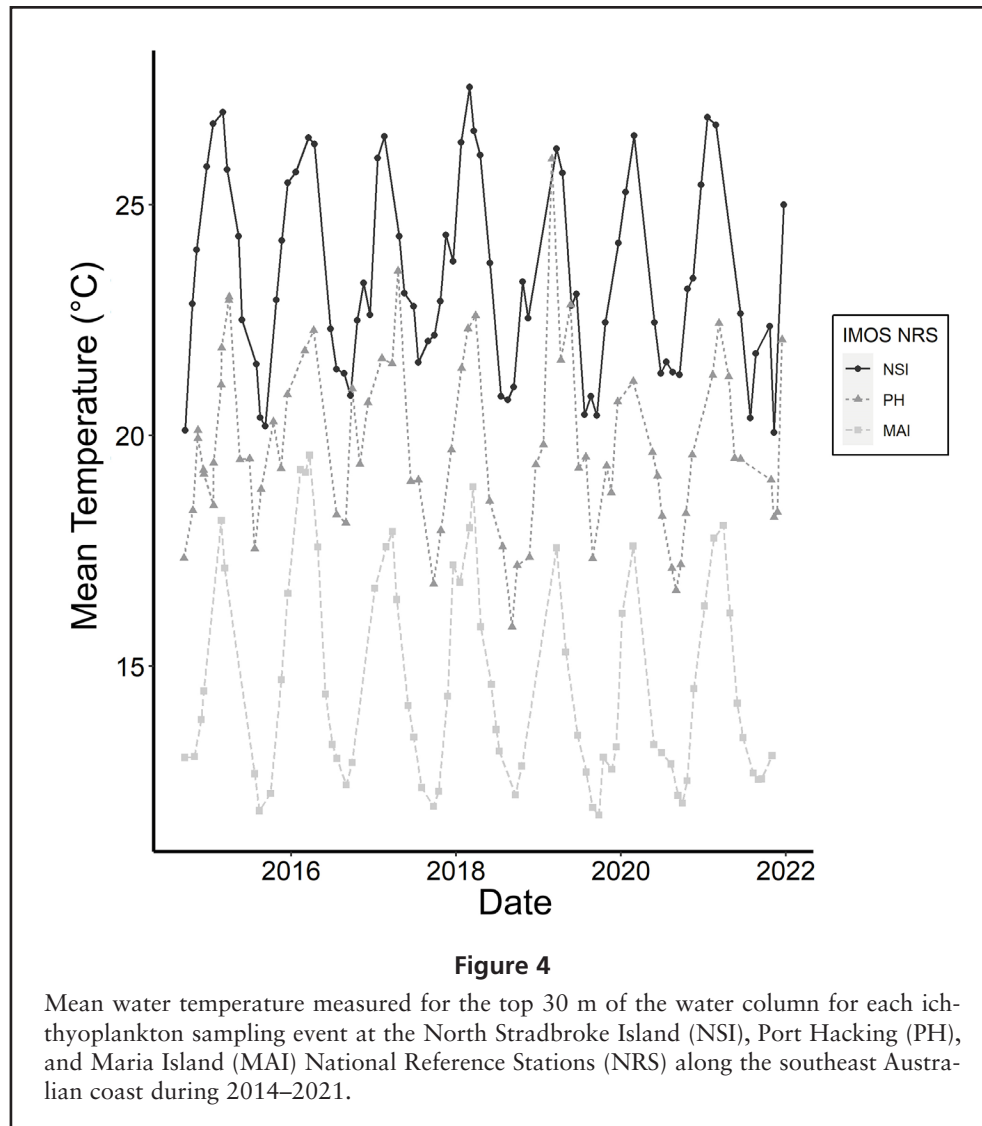
Figure 3

Gaussian copula latent variable ordination plot comparing flatfish larvae assemblages with seasons at the North Strad-broke Island (NSI), Port Hacking (PH), and Maria Island (MAI) National Reference Stations (NRS). Each vector corresponds to the factor loadings of a larval flatfish taxonomic group, with the length and direction corresponding to the amount of variance explained by that taxonomic group on the overall assemblage (i.e., a longer vector suggests that taxon explains a higher proportion of variance). Ichthyoplankton samples were collected monthly during 2014–2021. The data were grouped into the following 3-month intervals: spring (Sp, September–November), summer (Su, December–February), autumn (Au, March–May), and winter (Wi, June–August).

sistently recorded the highest chlorophyll values due to intrusions of cold, nutrient-rich water uplifted from the continental slope during spring and summer (Suppl. Fig. 4) (Tranter et al., 1986). Lower chlorophyll values were recorded at Maria Island, and the lowest values were recorded at North Stradbroke Island.

The PC analysis showed a clear distinction between the physical variables recorded at the 3 NRSs (Fig. 5, Suppl. Fig. 5). The samples taken at Maria Island were largely separated from both Port Hacking and North Stradbroke Island along the PC1 axis, which accounted for 47.6% of the total explained variance (Fig. 5). Both temperature and salinity contributed the most to the factor loadings of PC1 (0.732 and 0.663, respectively; Suppl. Table 3). The samples taken at Port Hacking

were also visually separated from both Maria Island and North Stradbroke along the PC2 axis, which accounted for a further 37.6% of the total explained variance (Fig. 5). Chlorophyll was the largest contributor to the factor loadings of PC2 (0.887, Suppl. Table 3), due to strong seasonal upwelling at Port Hacking.

Larval flatfish relationships with water temperature and salinity

The GLM results showed that the larval flatfish assemblage composition differed significantly across all 3 physical parameters. Temperature (Dev=618.4, P<001) and chlorophyll (Dev=101.3, P<0.001) had a higher impact on assemblage composition than salinity (Dev=28.6, P=0.032) (Suppl. Table 4). Plots of flatfish taxa concen-

Figure 4

Mean water temperature measured for the top 30 m of the water column for each ichthyoplankton sampling event at the North Stradbroke Island (NSI), Port Hacking (PH), and Maria Island (MAI) National Reference Stations (NRS) along the southeast Australian coast during 2014–2021.

trations versus temperature and salinity also showed that water temperatures were more influential in determining larval distribution patterns than salinity (Fig. 6). For bothids, the tropical genera intermediate flounder, *Crossorhombus* spp., *Engyprosopon* spp., and *Grammatobothus* spp. mainly occurred at water temperatures >20°C, reflecting their abundances at North Stradbroke Island. Crested flounder larvae generally occurred at water temperatures of 14–20°C, reflecting their abundances at Port Hacking and Maria Island. Low numbers of *Arnoglossus* spp. larvae occurred over the entire temperature range, and this is probably due to the occurrence of different tropical and temperate species of *Arnoglossus* at the 3 NRSs (FISHMAP; Rees et al., 2022). The other taxa (cynoglossids, *Pseudorhombus* spp., soleids, and samarids) occurred over a broad temperature range (18–26°C), which reflects their abundances at North Strad

broke Island and Port Hacking. Pleuronectid larvae were caught at the lowest water temperatures and salinities, which occurred around Maria Island.

Discussion

Latitudinal comparison of larval flatfish diversity and abundance

Compared with most previous studies in the region, which only identified flatfish larvae to family, this study identified larvae of the bothids crested flounder and intermediate flounder to the species level and the rest to the genus or family level. Even at this level of identification, distinct latitudinal, interannual, and seasonal differences were found in the number of flatfish larvae taxa, abundances, and larval assemblages at the 3 NRSs along
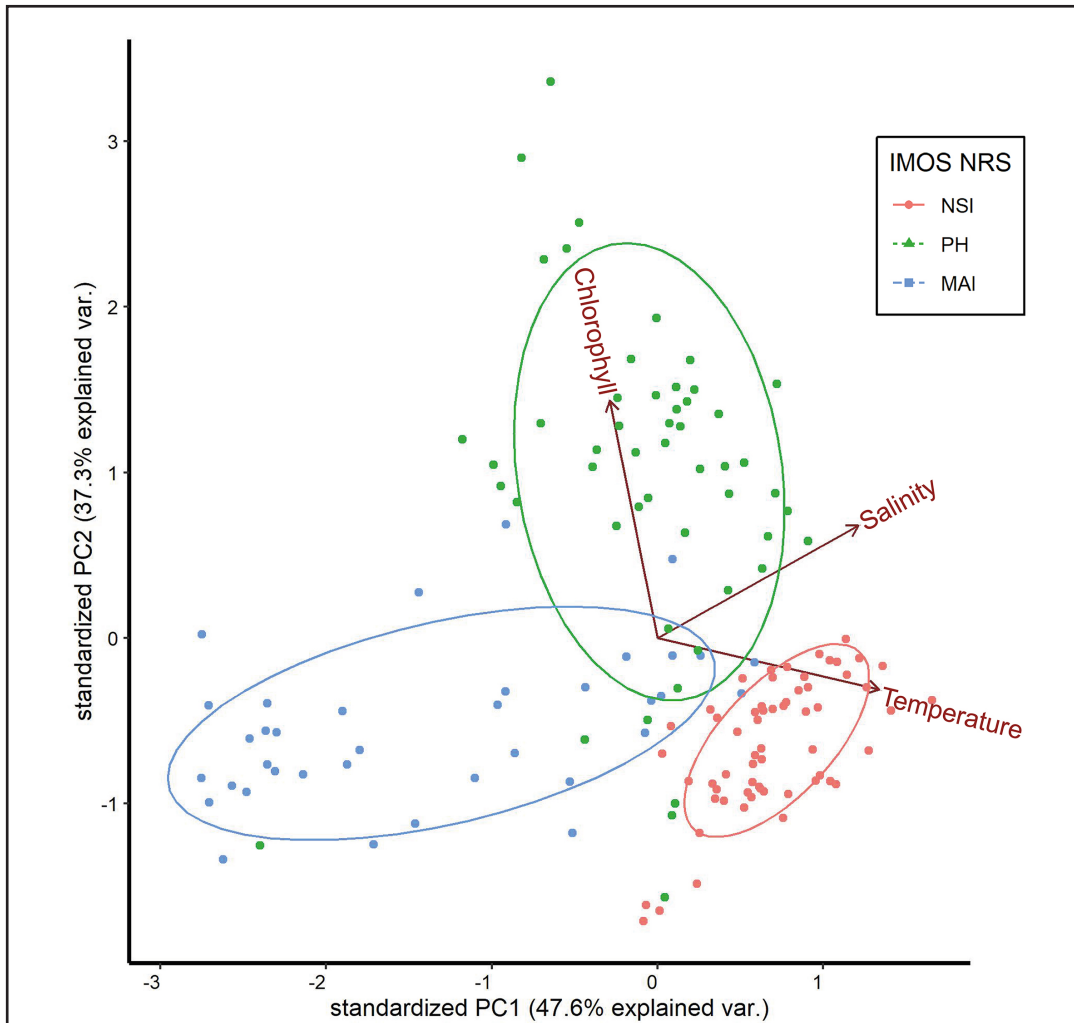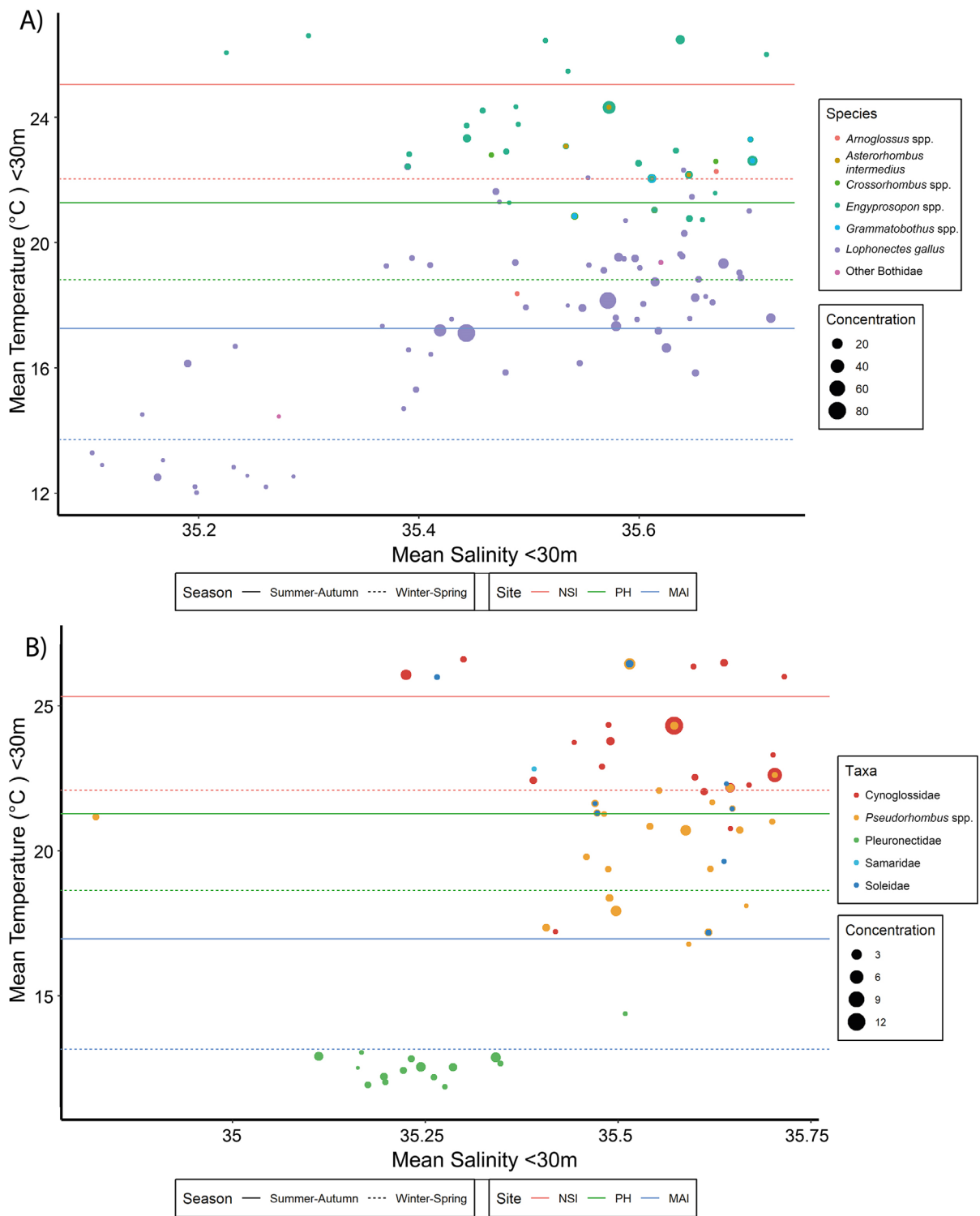
Figure 5

Principal component analysis (PCA) comparing water temperature, salinity, and chlorophyll for each ichthyoplankton sampling event at North Stradbroke Island (NSI, red circles), Port Hacking (PH, green triangles), and Maria Island (MAI, blue squares) National Reference Stations (NRS) during 2014–2021. The vectors correspond to the direction and magnitude of these 3 physical variables projected onto the space defined by PC1 (on the *x*-axis) and PC2 (on the *y*-axis). The more parallel a vector is with one of these 2 axes, the more that PC incorporates the variation (var.) of that physical variable. The longer a vector is, the more of the variation in that physical variable is captured in the 2-dimensional PCA plot. The confidence ellipses are arranged around the centroid of each site group and indicate the 95% confidence interval of each group within the PCA.

the southeast Australian coast. The pattern of decreasing diversity with latitude reflects the decrease in diversity of adult flatfish taxa with latitude (FISHMAP; Rees et al., 2022) and the overall decline in abundances and diversity in larval fish assemblages along the coast (Hinchliffe et al., 2021).

Larval flatfish assemblages at North Stradbroke Island and Port Hacking had a similar number of taxa but with varying abundances of bothid, cynoglossid, *Pseudorhom-*

bus spp., samarid, and soleid larvae. Tropical bothid genera that were abundant at North Stradbroke Island only occurred at low abundances at Port Hacking, probably due to northern spawning and subsequent southward transport of larvae in the EAC and the associated eddies, a pattern common to many species in this region (Schilling et al., 2020). This pattern highlights the importance of the EAC in transporting larvae of tropical species to temperate regions outside the normal adult distribution

Figure 6

Relationship of larval concentration (individuals/100 m³) to temperature and salinity of (**A**) 6 genera of Bothidae larvae and (**B**) Cynoglossidae, Paralichthyidae (*Pseudorhombus* spp.), Pleuronectidae, Samaridae, and Soleidae larvae sampled at North Stradbroke Island (NSI), Port Hacking (PH), and Maria Island (MAI) National Reference Stations (NRS) during 2014–2021. Solid and dotted lines represent the mean water temperature at the 3 stations during the summer to autumn season and the winter to spring season, respectively.

(Keane and Neira, 2008; Vergés et al., 2014). The presence of preflexion cynoglossid, *Pseudorhombus* spp., and soleid larvae indicates that spawning is probably occurring near both stations, while the larger samarid larvae at Port Hacking may have been transported south by the EAC. The lowest number of flatfish larvae taxa occurred at Maria Island. Crested flounder and pleuronectid larvae dominated the assemblage at this station, reflecting their southern Australian distribution (FISHMAP; Rees et al., 2022).

For previous broadscale larval fish surveys in southeast Australia, the most abundant flatfish family was Bothidae. Keane and Neira (2008) reported that unidentified bothids occurred in their northern survey transects in EAC waters, while crested flounder larvae only occurred in the mixed and TAS water masses in their southern transects. Mullaney et al. (2011) sampled in the EAC, the separation zone, and along the Tasman Front, while Mullaney and Suthers (2013) and Matis et al. (2014) sampled various oceanographic features, including anticyclonic and cyclonic eddies along the New South Wales coast. In these surveys, tropical bothid larvae, mainly *Engyprosopon* spp. and *Grammatobothus* spp., generally occurred in warmer waters of the EAC, separation zone, and in eddies and were absent in cooler coastal waters below the separation zone (A. Miskiewicz, personal observ.). In contrast, these surveys have associated crested flounder larvae with cooler water in the EAC separation zone, Tasman front, and eddies in the TAS. *Pseudorhombus* spp., cynoglossid larvae, and soleid larvae mainly occurred in the northern coastal EAC waters and not in the Tasman Front or eddies. For surveys in the Sydney region (Gray and Miskiewicz, 2000), the majority of bothid larvae in the samples were crested flounder (A. Miskiewicz, personal observ.), and there were low abundances of cynoglossid, *Pseudorhombus* spp., and soleid larvae, indicating localized spawning. In Victorian waters off of southern Australia, pleuronectid larvae have been caught in Port Phillip Bay (Jenkins, 1986; Neira and Sporcic, 2002) and Westernport Bay and Bass Strait (Kent et al., 2013).

Seasonal trends in larval flatfish assemblages and distributions

Although flatfish larvae were caught throughout the year, the abundances of different taxa varied seasonally among the 3 NRSs. At North Stradbroke Island, peaks in abundance of flatfish larvae occurred in summer and autumn, with the lowest abundances in winter. Peaks in abundance of the common bothids *Crossorhombus* spp., *Engyprosopon* spp., and *Grammatobothus* spp. usually occurred in summer and autumn, but seasonal peaks varied between the 8 years of sampling.

At Port Hacking, low abundances of tropical bothid larvae occurred in summer and autumn, when the southward flowing EAC extension was strongest. Crested flounder larvae were caught in all seasons, with the highest abundance occurring from autumn through spring. In contrast, the highest abundance of crested flounder at Maria Island occurred in summer, with none in winter. This trend indicates that there may be a temperature-driven latitudinal lag in spawning times related to water temperatures. At North Stradbroke Island and Port Hacking, cynoglossid, *Pseudorhombus* spp., and soleid larvae had similar summer and autumn abundance peaks but with variability between years. Gray and Miskiewicz (2000) and Keane and Neira (2008) reported similar seasonal patterns of abundance for these taxa.

At Maria Island, the highest abundances of pleuronectid larvae occurred in winter and spring, with none in summer. In Victorian waters, north of Maria Island, pleuronectid larvae have been caught from April to October (Jenkins, 1986), from February to September, with a peak abundance in March, in Port Phillip Bay (Neira and Sporcic, 2002), and from January to November in the nearby Westernport Bay and Bass Strait (Kent et al., 2013).

Distribution of larval flatfish taxa in relation to environmental variables

Markedly different larval flatfish assemblages were caught at the 3 NRSs, corresponding to the distinctive mean and seasonal water temperature ranges. In the tropical waters off Townsville (18°S), Liew (1983) reported that larvae of different species of bothids and paralichthyids had different seasonal abundance patterns, indicating differences in spawning strategies related to seasonal variation in water temperatures and salinities in the region. Keane and Neira (2008) identified 3 major recurrent larval fish assemblages off southeast Australia that matched each of 3 water masses in the region. These were the northern EAC (20.5–23.4°C), the southern TAS (14.8–17.5°C), and a mixed EAC–TAS water mass (18.3–19.9°C) located between the other 2, as detailed by Keane and Neira (2008). The North Stradbroke Island NRS was located within the EAC, the Port Hacking NRS within the EAC–TAS, and the Maria Island NRS within the TAS water masses, respectively.

In this study, the tropical bothids intermediate flounder, *Crossorhombus* spp., *Engyprosopon* spp., and *Grammatobothus* spp., and samarids were strongly linked to warmer water associated with the EAC. In contrast, crested flounder larvae were associated with the cooler EAC–TAS and TAS water masses. Tropical and temperate taxa, cynoglossids, *Pseudorhombus* spp., and soleids, were associated with both the EAC and EAC–TAS water masses, reflecting their abundances at North Stradbroke Island and Port Hacking. There was

also some evidence of a latitudinal lag in larval abundance of crested flounder between NRSs, with the highest abundance in winter at Port Hacking and in summer at Maria Island. None were caught in winter. This lag may be driven by different spawning times across different local temperatures (Neuheimer et al., 2018).

Directions for future study

Eastern Australia is a hot spot of biological change driven by climate change and tropicalization (Johnson et al., 2011; Vergés et al., 2014). Long-term monitoring programs are invaluable for detecting trends in fish phenology (Asch, 2015), interannual variation in assemblage composition (Peabody et al., 2018), and seasonal and long-term changes in ichthyoplankton assemblages related to climate change (Koslow and Couture, 2013). Changes to flatfish larvae dispersal and phenology may be occurring as a result of changes in current and upwelling dynamics in the EAC (Wu et al., 2012; Malan et al., 2021) as in other systems (Asch, 2015; Peabody et al., 2018), which may alter the seasonality of assemblage compositions. While no significant interannual trends in larval flatfish taxa were found over the 8 years of the IMOS larval fish monitoring program, this study establishes an important baseline for future changes in larval flatfish phenology and assemblages in eastern Australia. The next step is to identify to species the flatfish larvae that were only classified to family or generic level to provide a finer level of detail in patterns of larval seasonality and distributions of larvae in samples from the NRSs. Undertaking specific identifications would be assisted by cytochrome *c* oxidase subunit 1 barcoding of the ethanol fixed-larvae from the NRS samples.

Conclusions

Eleven taxa of flatfish larvae were caught in ichthyoplankton samples collected monthly over 8 years at 3 NRSs along the southeast Australian coast. This study found that the larval flatfish assemblages differed between the NRSs, and these differences were related to the occurrence of different water masses along the coast. The highest number of flatfish larvae taxa occurred in warmer tropical waters. The number of larvae decreased with increasing latitude and colder water temperatures, with the lowest number caught at the southern NRS. The abundances of different taxa varied seasonally, and the assemblage composition varied between seasons and years but with no overall change in abundances over the 8 years of the study. This study establishes a baseline for assessing future changes in larval fish assemblages due to climate change in eastern Australia.

Literature cited

Asch, R. G.
    2015. Climate change and decadal shifts in the phenology of larval fishes in the California Current ecosystem. Proc. Natl. Acad. Sci. 112(30):E4065–E4074. https://doi.org/10.1073/pnas.1421946112
Bailey, K. M., and S. J. Picquelle.
    2002. Larval distribution of offshore spawning flatfish in the Gulf of Alaska: potential transport pathways and enhanced onshore transport during ENSO events. Mar. Ecol. Prog. Ser. 236:205–217. https://doi.org/10.3354/meps236205
Bailey, K. M., H. Nakata, and H. W. Van der Veer.
    2005. The plankton stages of flatfishes: physical and biological interactions in transport processes. *In* Flatfishes: biology and exploitation (R. N. Gibson, ed.), p. 94–119. Blackwell Sci., Oxford, UK.
Bailey, K. M., A. A. Abookire, and J. T. Duffy-Anderson.
    2008. Ocean transport paths for the early life history stages of offshore-spawning flatfishes: a case study in the Gulf of Alaska. Fish Fish. 9:44–66. https://doi.org/10.1111/j.1467-2979.2007.00268.x
Bakun, A.
    2006. Fronts and eddies as key structures in the habitat of marine fish larvae: opportunity, adaptive response and competitive advantage. Sci. Mar. 70(S2):105–122. https://doi.org/10.3989/scimar.2006.70s2105
Cetina-Heredia, P., M. Roughan, E. van Sebille, and M. A. Coleman.
    2014. Long-term trends in the East Australian Current separation latitude and eddy driven transport. J. Geophys. Res. Oceans 119:4351–4366. https://doi.org/10.1002/2014JC010071
Crawford, C. M.
    1986. Development of eggs and larvae of the flounders *Rhombosolea tapirina* and *Ammotretis rostratus* (Pisces: Pleuronectidae). J. Fish Biol. 29:325–334. https://doi.org/10.1111/j.1095-8649.1986.tb04949.x
Cresswell, G.
    2000. Currents of the continental shelf and upper slope of Tasmania. Pap. Proc. R. Soc. Tasman. 133(3):21–30. https://doi.org/10.26749/rstpp.133.3.21
Davies, C., and E. Sommerville (eds.).
    2020. National reference stations biogeochemical operations manual, vers. 3.3.1, 66 p. Integr. Mar. Obs. System. https://doi.org/10.26198/5c4a56f2a8ae3
Fukui, A., M. Suzuki, Y. Suzuki, and I. Uotani.
    2002. Early ontogeny of *Lophonectes gallus* (Bothidae) from southeastern Australia. Ichthyol. Res. 49:159–164. https://doi.org/10.1007/s102280200021
Garcia, V., H. T. Schilling, D. O. Cruz, S. M. Hawes, J. D. Everett,

M. Roughan, A. G. Miskiewicz, E. A. Pakhomov, A. Jeffs, and I. M. Suthers.
2022. Entrainment development of larval fish assemblages in two contrasting cold core eddies of the East Australian Current system. Mar. Ecol. Prog. Ser. 685:1–18. https://doi.org/10.3354/meps13982

Gomon, M. F., D. J. Bray, and R. H. Kuiter (eds.).
2008. Fishes of Australia's southern coast, 928 p. New Holland Publ., Wahroonga, NSW, Australia.

Gray, C. A., and A. G. Miskiewicz.
2000. Larval fish assemblages in south-east Australian coastal waters: seasonal and spatial structure. Estuar. Coastal Shelf Sci. 50:549–570. https://doi.org/10.1006/ecss.1999.0595

Hare, J. A., M. P. Fahay, and R. K. Cowen.
2001. Springtime ichthyoplankton of the slope region off the north-eastern United States of America: larval assemblages, relation to hydrography and implications for larval transport. Fish. Oceanogr. 10:164–192. https://doi.org/10.1046/j.1365-2419.2001.00168.x

Hill, K. L., S. R. Rintoul, R. Coleman, and K. R. Ridgway.
2008. Wind forced low frequency variability of the East Australia Current. Geophys. Res. Lett. 35:L08602. https://doi.org/10.1029/2007GL032912

Hinchliffe, C., J. A. Smith, J. D. Everett, D. S. Falster, A. Lara-Lopez, A. G. Miskiewicz, A. J. Richardson, H. T. Schilling, and I. M. Suthers.
2021. Modelling the distribution of larval fish in a western boundary current using a multi-voyage database. Rev. Fish Biol. Fish. 31:399–415. https://doi.org/10.1007/s11160-021-09647-x

Horwood, J., D. Cushing, and T. Wyatt.
2000. Planktonic determination of variability and sustainability of fisheries. J. Plankton Res. 22:1419–1422. https://doi.org/10.1093/plankt/22.7.1419

Jenkins, G. P.
1986. Composition, seasonality and distribution of ichthyoplankton in Port Phillip Bay, Victoria. Aust. J. Mar. Freshw. Res. 37:507–520. https://doi.org/10.1071/MF9860507

Johnson, C. R., S. C. Banks, N. S. Barrett, F. Cazassus, P. K. Dunstan, G. J. Edgar, S. D. Frusher, C. Gardner, M. Haddon, F. Helidoniotis, et al.
2011. Climate change cascades: shifts in oceanography, species' ranges and subtidal marine community dynamics in eastern Tasmania. J. Exp. Mar. Biol. Ecol. 400:17–32. https://doi.org/10.1016/j.jembe.2011.02.032

Keane, J. P., and F. J. Neira.
2008. Larval fish assemblages along the south-eastern Australian shelf: linking mesoscale non-depth-discriminate structure and water masses. Fish. Oceanogr. 17:263–280. https://doi.org/10.1111/j.1365-2419.2008.00478.x

Kent, J., G. Jenkins, and S. Acevedo.
2013. Temporal and spatial patterns in ichthyoplankton assemblages in bay and open coastal environments. J. Fish Biol. 82:408–429. https://doi.org/10.1111/jfb.12008

Koslow, J. A., and J. Couture.
2013. Ocean sciences: follow the fish. Nature 502:163–164. https://doi.org/10.1038/502163a

Last, P. R., W. T. White, D. C. Gledhill, J. J. Pogonoski, V. Lyne, and N. J. Bax.
2011. Biogeographical structure and affinities of the marine demersal ichthyofauna of Australia. J. Biogeogr. 38:1484–1496. https://doi.org/10.1111/j.1365-2699.2011.02484.x

Liew, H.-C.
1983. Studies on flatfish larvae (fam. Psettodidae and Bothidae, Pleuronectiformes) in the shelf waters of the central Great Barrier Reef, Australia. M.S. thesis, 186 p. James Cook Univ., Townsville, Australia. [Available from Universiti Putra Malaysia, 43400 UPM Serdang, Selangor Darul Ehsan, Malaysia.]
1986. The identity of eleven species of larval flatfishes off Townsville, Australia, and use of a clustering method to identify two unknown types. In Indo-Pacific fish biology: proceedings of the second international conference on Indo-Pacific fishes (T. Uyeno, R. Arai, T. Taniuchi, and K. Matsuura, eds.), p. 715–727. Ichthyol. Soc. Jpn., Tokyo, Japan.

Liew, H.-C., N. E. Milward, and R. F. Hartwick.
1988. Descriptions of larval flatfishes of the genera *Psettodes* (Psettodidae) and *Pseudorhombus* (Paralichthyidae) from the Great Barrier Reef, Australia. Aust. J. Mar. Freshw. Res. 39:51–70. https://doi.org/10.1071/MF9880051

Malan, N., M. Roughan, and C. Kerry.
2021. The rate of coastal temperature rise adjacent to a warming western boundary current is nonuniform with latitude. *Geophys. Res. Lett. 48:e2020GL090751.* https://doi.org/10.1029/2020GL090751

Matis, P. A., W. F. Figueira, I. M. Suthers, J. Humphries, A. Miskiewicz, R. A. Coleman, B. P. Kelaher, and M. D. Taylor.
2014. Cyclonic entrainment? The ichthyoplankton attributes of three major water mass types generated by the separation of the East Australian Current. ICES J. Mar. Sci. 71:1696–1705. https://doi.org/10.1093/icesjms/fsu062

Mullaney, T. J., and I. M. Suthers.
2013. Entrainment and retention of the coastal larval fish assemblage by a short-lived, submesoscale, frontal eddy of the East Australian Current. Limnol. Oceanogr. 58:1546–1556. https://doi.org/10.4319/lo.2013.58.5.1546

Mullaney, T. J., A. G. Miskiewicz, M. E. Baird, P. T. P. Burns, and I. M. Suthers.
2011. Entrainment of larval fish assemblages from the inner shelf into the East Australian Current and into the western Tasman Front. Fish. Oceanogr. 20:434–447. https://doi.org/10.1111/j.1365-2419.2011.00594.x

Neira, F. J., and M. I. Sporcic.
2002. Use of ichthyoplankton ecology to evaluate ecosystem changes: a case study in a large, semi-enclosed Australian bay. Mar. Freshw. Res. 53:339–354. https://doi.org/10.1071/MF01111

Neuheimer, A. B., B. R. MacKenzie, and M. R. Payne.
2018. Temperature-dependent adaptation allows fish to meet their food across their species' range. Sci. Adv. 4:eaar4349. https://doi.org/10.1126/sciadv.aar4349

Oke, P. R., M. Roughan, P. Cetina-Heredia, G. S. Pilo, K. R. Ridgway, T. Rykova, M. R. Archer, R. C. Coleman, C. G. Kerry, C. Rocha, et al.
2019. Revisiting the circulation of the East Australian Current: its path, separation, and eddy field. Prog. Oceanogr. 176: 102139. https://doi.org/10.1016/j.pocean.2019.102139

Okiyama, M. (ed.)
2014. An atlas of early stage fishes in Japan, 2nd ed., 1896 p. Tokai Univ. Press, Hadano, Japan. [In Japanese.]

Ozawa, T., and A. Fukui.
1986. Studies on the development and distribution of the

bothid larvae in the western North Pacific. *In* Studies on the oceanic ichthyoplankton in the Western North Pacific (T. Ozawa, ed.), p. 322–420. Kyushu Univ. Press, Fukuoka, Japan.

Pauly, D.
1994. A framework for latitudinal comparisons of flatfish recruitment. Neth. J. Sea Res. 32:107–118. https://doi.org/10.1016/0077-7579(94)90035-3

Peabody, C. E., A. R. Thompson, D. F. Sax, R. E. Morse, and C. T. Perretti.
2018. Decadal regime shifts in southern California's ichthyoplankton assemblage. Mar. Ecol. Prog. Ser. 607:71–83. https://doi.org/10.3354/meps12787

Popovic, G. C., D. I. Warton, F. J. Thomson, F. K. C. Hui, and A. T. Moles.
2019. Untangling direct species associations from indirect mediator species effects with graphical models. Methods Ecol. Evol. 10:1571–1583. https://doi.org/10.1111/2041-210X.13247

R Core Team.
2021. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. [Available from https://www.R-project.org/, accessed July 2022.]

Rees, A. J. J., G. K. Yearsley, K. Gowlett-Holmes, and J. Pogonoski.
2022. Codes for Australian aquatic biota (on-line version). CSIRO National Collections and Marine Infrastructure (formerly CSIRO Marine and Atmospheric Research). World Wide Web electronic publication, 1999 onwards. [Available from https://www.marine.csiro.au/data/caab/.]

Rodriguez, J. M.
2019. Assemblage structure of ichthyoplankton in the NE Atlantic in spring under contrasting hydrographic conditions. Sci. Rep. 9:8636. https://doi.org/10.1038/s41598-019-44918-5

Roughan, M., H. S. Macdonald, M. E. Baird, and T. M. Glasby.
2011. Modelling coastal connectivity in a Western Boundary Current: seasonal and inter-annual variability. Deep Sea Res., II 58:628–644. https://doi.org/10.1016/j.dsr2.2010.06.004

Schilling, H. T., J. D. Everett, J. A. Smith, J. Stewart, J. M. Hughes, M. Roughan, C. Kerry, and I. M. Suthers.
2020. Multiple spawning events promote increased larval dispersal of a predatory fish in a western boundary current. Fish. Oceanogr. 29:309–323. https://doi.org/10.1111/fog.12473

Smith, J. A., A. G. Miskiewicz, L. E. Beckley, J. D. Everett, V. Garcia, C. A. Gray, D. Holliday, A. R. Jordan, J. Keane, A. Lara-Lopez, et al.
2018. A database of marine larval fish assemblages in Australian temperate and subtropical waters. Sci. Data 5:180207. https://doi.org/10.1038/sdata.2018.207

Tranter, D. J., D. J. Carpenter, and G. S. Leech.
1986. The coastal enrichment effect of the East Australian Current eddy field. Deep. Sea Res. Oceanogr., A 33:1705–1728. https://doi.org/10.1016/0198-0149(86)90075-0

Vergés, A., P. D. Steinberg, M. E. Hay, A. G. B. Poore, A. H. Campbell, E. Ballesteros, K. L. Heck Jr., D. J. Booth, M. A. Coleman, D. A. Feary, et al.
2014. The tropicalization of temperate marine ecosystems: climate-mediated changes in herbivory and community phase shifts. Proc. R. Soc., B 281:20140846. https://doi.org/10.1098/rspb.2014.0846

Wang, Y., U. Naumann, S. T. Wright, and D. I. Warton.
2012. mvabund—an R package for model–based analysis of multivariate abundance data. Methods Ecol. Evol. 3:471–474. https://doi.org/10.1111/j.2041-210X.2012.00190.x

Wu, L., W. Cai, L. Zhang, H. Nakamura, A. Timmermann, T. Joyce, M. J. McPhaden, M. Alexander, B. Qiu, M. Visbeck, P. Chang, and B. Giese.
2012. Enhanced warming over the global subtropical western boundary currents. Nat. Clim. Change 2:161–166. https://doi.org/10.1038/nclimate1353