Regional-scale surface temperature variability allows prediction of Pacific bluefin tuna recruitment

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Future sustainable management of fisheries will require resilience to the effects of environmental variability and climate change on stock productivity. In this study, we examined relationships between sea surface temperature (SST) in the region between Taiwan and the Sea of Japan, and annual recruitment of Pacific bluefin tuna (*Thunnus orientalis*: PBF) over the past 35 years. Spatial correlation maps showed that warmer SSTs south of Shikoku, in the East China Sea and in the Sea of Japan from summer to late fall were associated with above average recruitment. SST anomalies near larval and juvenile habitats were most strongly correlated with local air temperatures. Generalized Additive Models predicting annual PBF recruitment from SST fields suggested that the influence of SST on recruitment was stronger than that of spawning stock biomass. Correlations between SST and recruitment likely reflect biological processes relevant to early juvenile habitat suitability. The influence of late fall SSTs could also be a result of varying availability of age-0 fish to the troll fishery; however, the relative importance of these processes was not clear. Despite these knowledge gaps, the strong predictive power of SST on PBF recruitment can allow more proactive management of this species under varying environmental conditions.

Keywords: fisheries oceanography, Generalized Additive Models, Pacific bluefin tuna

Introduction

Although the stock–recruitment relationship (SRR) is a central principle of fisheries management (Hilborn and Walters, 1992), it is widely acknowledged that environmental factors can and do drive substantial variability in recruitment. In many species, recruitment appears to vary largely independent of spawning stock biomass (SSB; Szuwalski *et al.*, 2015; Lowerre-Barbieri *et al.*, 2017), or to change its relationship with spawning biomass over time (Megrey *et al.*, 2005; Britten *et al.*, 2016).

Climate change is contributing to largely unprecedented conditions in some marine ecosystems (Hoegh-Guldberg and Bruno, 2010), and further directional change is likely in the future. Fisheries management processes must therefore become increasingly able to adapt to environmentally driven shifts in stock productivity and distribution (Grafton, 2010; Koehn *et al.*, 2011). This can be achieved through several strategies, including environmentally informed reference points and indices, and development of broader ecosystem-based management frameworks (Punt *et al.*, 2013; DePiper *et al.*, 2017). While there is a large body of research linking environmental conditions to distribution of various life stages of fish species in the context of climate change (e.g. Cheung *et al.*, 2010; Hazen *et al.*, 2013), a key remaining question is how recruitment might change in the future. This knowledge is essential to assess performance of current and alternative management strategies under climate change, and to develop environmentally informed management benchmarks.

There is a long history of fisheries oceanography studies linking environmental conditions to recruitment in exploited fishes (e.g. Houde, 2008; Rothschild, 2000; Planque and Frédou, 1999; Megrey et al., 2005). However, these relationships often fail when later retested with new data, or different analysis techniques (Myers, 1998). As a result, the adoption of ecosystem-based fisheries management has been somewhat hampered by the lack of robust correlates with key variables such as recruitment, as well as limited process-based understanding of how environmental variability drives recruitment in different species. Nevertheless, simulations suggest that, if a robust relationships between environmental conditions and recruitment exists, incorporation of environmental predictors into the assessment process could provide early warnings of falling stock productivity, allowing for more effective fisheries management, and higher yields (e.g. Tommasi et al., 2017a).

Similar to most managed stocks, status of Pacific bluefin tuna (PBF: *Thunnus orientalis*) is currently assessed without explicit consideration of environmental effects. PBF range throughout the North Pacific Ocean (Fujioka et al., 2016), but their spawning grounds are primarily restricted to two small areas in the western Pacific: between the Philippines and northern Nansei Islands between April and June, and in the Sea of Japan during July and August (Tanaka and Suzuki, 2016; Ohshimo et al., 2017). Annual recruitment is estimated from a standardized index of troll fishery catches of young-of-the-year fish from around Nagasaki Prefecture in the fall–spring following spawning (Yamada et al., 2006; ISC, 2016). Recruitment was generally low prior to 1990, higher from 1994 to 2008, and has been declining since then (Figure 1).

Some recent studies have suggested that PBF recruitment variability is linked to the ocean environment, in particular to the Pacific Decadal Oscillation (PDO; Sakuramoto, 2016; Harford et al., 2017). The PDO arises from a number of different physical processes, related to the El Nino-Southern Oscillation cycle (ENSO), random fluctuations in the Aleutian Low, oceanic thermal inertia, and decadal-scale changes in the Kuroshio–Oyashio current system (Newman et al., 2016). During positive phases of the PDO, SSTs are warmer than average along the west coast of North America, and in the tropical eastern Pacific, and cooler than average at mid-latitudes in the central and western North Pacific, including coastal Japan. This suggests that the PDO may influence PBF recruitment via its effects on SST, which was recently supported by Ishida et al. (2018).

Other processes can also influence ocean conditions near to PBF early life habitats, and thus may be important for recruitment predictability. El Niño events are associated with negative SST anomalies in the western North Pacific, which are strongest along ∼40°N, but weaker negative anomalies are also present around coastal Japan during the summer and fall (Alexander et al., 2002, 2004). Other potential contributors to regional SST variability include the strength of the Asian monsoons, and the Arctic Oscillation (AO; Minobe et al., 2004; Ohshimo et al., 2009).

Despite these advances, several questions remain. The PDO is a basin-scale index, and the SST measures used in Ishida et al. (2018) were spatially and temporally coarse (averaged quarterly across regions $>200\,000\,km^2$). It is therefore not clear where and when SST is related to PBF recruitment, which life stages are most strongly affected, and if the effects are common to both spawning grounds. Watai et al. (2017) concluded that only PBF larvae with fast, steady growth survive to be juveniles. Temperature is well known to positively influence larval tuna growth (e.g. Kimura et al., 2010; Satoh et al., 2013, 2014), but other factors such as prey abundance

and composition, and larval transport via ocean currents may also be important (Kimura et al., 2010; Satoh et al., 2014; Tanaka et al., 2014). It is generally hypothesized that survival during the larval and post-larval phases is most important in determining year class strength in pelagic fishes (e.g. Bailey and Houde, 1989; Hare and Cowen, 1997). However, Ishida et al. (2018) found stronger correlations between regional SST and PBF recruitment in summer and fall. While spawning on the northern spawning ground extends through August, by the fall all surviving PBF are well into the juvenile stage. Alternatively, SST may be influencing the PBF recruitment index (rather than recruitment itself) by changing the availability of age-0 juveniles to the troll fishery. The effects of SST on the distribution and movement of small juvenile PBF fitted with satellite tags has been noted previously (Kitagawa et al., 2006), and proposed as a potential influence on catches in the fishery (Ichinokawa et al., 2014).

In this study, we aimed to address these knowledge gaps by exploring finer-scale relationships between spatiotemporal SST variability, and PBF recruitment estimates from the most recent stock assessment. We then used these findings to develop multivariate, non-linear models to define the overall predictability of annual PBF recruitment from ocean conditions around spawning and nursery grounds.

Material and methods

A schematic of the workflow linking the data sources and models described below is shown in Supplementary Figure S1.
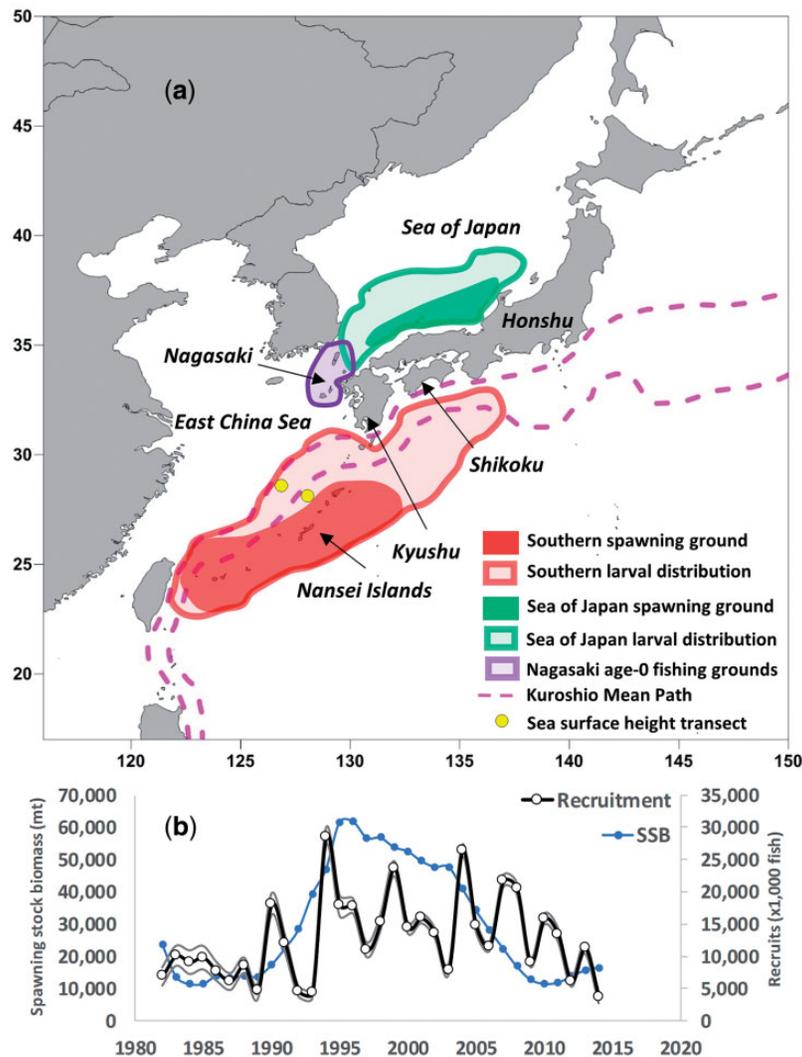
Biological time series

We obtained annual estimates of female SSB and recruitment from the 2016 PBF stock assessment report (ISC, 2016). Population dynamics were estimated for the assessment using a fully integrated age-structured model (Stock Synthesis v3.24f), which was fit to catch, size-composition and catch-per-unit-effort (CPUE) data from 1952 to 2015. However, we only used spawning biomass and recruitment values since 1982 in this study, to match the period when both SST and recruitment estimates were likely most reliable (Ishida et al., 2018). We used values from the base-case model only, which assumes that there is essentially no SRR for PBF, and thus that the curvature of the SRR relationship (steepness) is 0.999 (ISC, 2016; Nakatsuka et al., 2017).

Temperature time series

We defined the study area as including locations where (i) adult PBF are known or likely to spawn, or (ii) where larvae or small juvenile PBF have been collected previously (Fujioka et al., 2016; Tanaka and Suzuki, 2016; Ohshimo et al., 2017; Figure 1). Monthly SSTs were extracted on a 1×1 degree grid, for all months between April and (the following) January each year between 1982 and 2014, and were obtained from the National Oceanographic and Atmospheric Administration (NOAA) Optimum Interpolation Sea Surface Temperature (OISST) analysis version 2 (Reynolds et al., 2002).

Spatiotemporal correlations

Environmental variables can influence recruitment in different ways across the geographic extent of a species reproductive range (e.g. Planque and Frédou, 1999). We therefore calculated the correlation between annual recruitment and SST at each $1 \times 1°$ grid point, in each month, across all years from 1982 to 2014. We evaluated both linear and simple non-linear correlations using 2nd order polynomials, as relationships between temperature and both

Figure 1. (a) Study area in the western North Pacific Ocean. Approximate spawning areas and larval distributions are shown, as well as the climatological path of the Kuroshio Current, and the two locations used for calculating Kuroshio Current strength, after Andres *et al.* (2008). The fishing grounds for the age-0 troll fishery, upon which the recruitment index is based, are shown near to Nagasaki. (b) Annual PBF recruitment with standard deviations and spawning stock biomass (SSB) from the stock assessment model, 1982–2014.

spawning activity and larval survival have previously been reported to be non-linear for PBF (e.g. Kimura *et al.*, 2010; Ohshimo *et al.*, 2017). These were fit using the "lm" routine in R 3.3.2. Results were visualized by plotting values at each grid point by month, using Surfer 9 (Golden Software). Months and locations with the highest correlations were then selected for further examination, to define the nature of the relationship between recruitment and SST in each area. Neighbouring grid points with stronger correlations were grouped together to form "Areas of Interest" (AOIs). Temporal autocorrelation can reduce the degrees of freedom of the sample correlation between time series. To assess the importance of temporal autocorrelation when comparing recruitment to mean SST within our AOIs, we calculated the strength and significance of the autocorrelation function (ACF) for SST within each AOI at lag 1 year.

Drivers of regional temperature variability

SST has been highlighted as a potential driver of PBF recruitment, but is temporally and spatially autocorrelated (Ishida *et al.*, 2018).

We therefore used Principal Components Analysis (PCA) to summarize the spatiotemporal variability. This technique reduces the dimensionality of multivariate data to principle modes of variation, and calculates a set of linearly uncorrelated variables (principle components), which summarize progressively less of the variance (Legendre and Legendre, 1998). We first calculated SST anomalies against longitude/latitude/month means from 1982 to 2014, to remove the seasonal signal. We then applied PCA to the full SST anomaly dataset using the "prcomp" routine in the "stats" package in R 3.3.2 (R Core Team, 2016).

We obtained time-series of climate indices from the NOAA Earth System Research Laboratory (Niño 3.4, PDO, AO) and the Japan Meteorological Agency (summer monsoon) at monthly resolution, and collapsed these into June–December means for each year from 1982 to 2014 (see Results for rationale behind selection of these months). Correlation coefficients were then calculated between mean values of the first four PCs, and means of each of the four climate indices. The significance of each

correlation was assessed using "lm" in R 3.3.2, with a Durbin–Watson test for temporal autocorrelation of residuals non-significant at $p < 0.05$ unless otherwise stated in the text.

We also included two local environmental indices: air temperature anomalies, and an index of Kuroshio Current transport. Air temperatures were obtained from the National Centers for Environmental Prediction/National Center for Atmospheric Research (NCEP/NCAR) Reanalysis at 2.5 latitude × longitude resolution (Kalnay *et al.*, 1996). We used values at 700 hPa, as near-surface air temperatures can be influenced by feedbacks from the surface ocean, and we were most interested in processes which drive SST. Anomalies of mean monthly values (1982–2014) were calculated for a box defined by 122.5–135°E, and 22.5–37.5°N. The Kuroshio Current transport index was calculated after Andres *et al.* (2008), who showed that the difference in sea surface height anomaly (SSHa) between two points near the Nansei Islands was strongly and linearly correlated with observed transport (Figure 1). SSHa values were extracted at the same points as in Andres *et al.* (2008), but we obtained them from the DUACS 2014 delayed time 0.25° gridded analysis provided by CMEMS, from 1993 to 2014, instead of using along-track measurements. However, results were very similar to those in Andres *et al.* (2008). The two local indices and four climate indices were not independent from each other, and shared common forcing mechanisms. However, we used them in an exploratory manner to show the potential influence of various processes on observed SST variability within the study area.

Predictive recruitment models

The effects of spatiotemporal SST variability across the early life habitats of PBF on recruitment were summarized using Generalized Additive Models (GAMs: Wood, 2006), which were built using the "mgcv" package in R 3.3.2. GAMs are similar to Generalized Linear Models, but incorporate smoothing functions of predictors, to allow non-linear relationships between predictors and response variables. They have been previously shown to perform well in estimating recruitment–environment relationships, when compared with linear models (Megrey *et al.*, 2005; Tommasi *et al.*, 2015).

We compared two approaches for predicting annual recruitment from regional SST. First, we derived SST time series from selected AOIs where SST correlated most strongly with recruitment, and used these as predictors in the GAM. This approach was conceptually simple and easy to interpret, but raised the potential problem of multicollinearity among predictors, as SST within the study area was highly auto-correlated in space and time. Secondly, we investigated using the first several PC axes as predictor variables in the GAM. Using PCs as predictors had the advantage of both summarizing SST conditions throughout the spawning season, and also providing variables that were uncorrelated to each other. However, this may come at the cost of increased difficulties with model interpretation. Each GAM also included annual SSB as a predictor. SSB was modelled to allow for a non-linear response (and hence density dependent effects) between SSB and recruitment. Annual estimated recruitment from the stock assessment report was used as the response variable.

GAMs were built using a quasi-Poisson error distribution with a log link function. We restricted the number of "knots" for polynomial smoothers, to ensure biologically realistic response curves,

and, and we used out-of-model validation to select the optimal value. This was done by training each GAM on the first 23 years of the time series (1982–2004), and then testing its accuracy on the last 10 years (2005–2014). Both time periods included both high and low recruitment years. The process was repeated for GAMs using a maximum of 3, 4, and 5 knots for smoothers, and the best model selected using the R^2 value on the unseen, out-of-model data. We used the Shapiro–Wilk test and visual examination to check that model residuals were roughly normally distributed, and showed no serious heterogeneity. Temporal autocorrelation of residuals was tested for using the Durbin–Watson test.

To provide predictions of potential PBF recruitment in years beyond the current stock assessment (2015 and 2016), OISST fields for those years were also extracted separately, and scored through both GAMs. SSB for 2015 and 2016 was held constant at 2014 levels for these predictions.
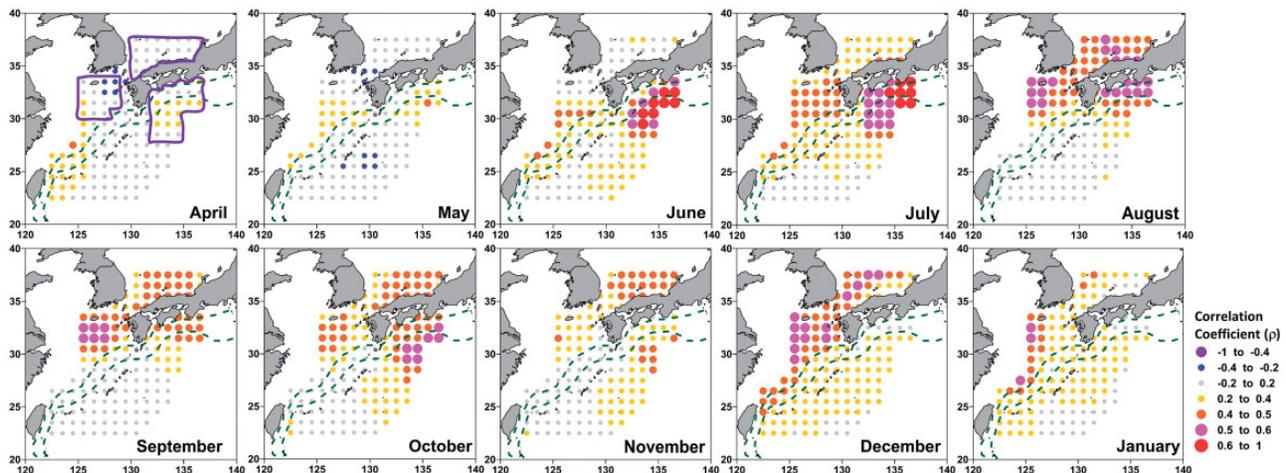
Results

Spatiotemporal correlations

Across all months and locations, the increase in skill gained by using 2nd order polynomial correlations over linear relationships was modest, with a mean R^2 increase of 0.02. The R^2 statistic improved by > 0.1 in only 2.6% of month/location combinations, and so we proceeded using linear relationships for the correlation maps. These showed that SST was positively associated with recruitment off the southern coast of Shikoku from June to October, in the East China Sea in July–October, and then again in December, and in the Sea of Japan during August–December. Nearly all correlations were positive, with the exception of some very weak negative relationships in April and May. The strongest correlations ($\rho > 0.6$) were found south of Shikoku in June and July (Figure 2).

We selected three AOIs based on the spatial patterns identified in Figure 2. The first was the area south of Shikoku, which is a juvenile nursery area for larvae spawned on the southern spawning ground (Figure 1). The second AOI was the southwest Sea of Japan, which encompasses larval and juvenile habitats for the northern spawning ground (Figure 1). The third AOI covered the northern East China Sea. Small juveniles from both spawning grounds may recruit to this habitat, and are targeted by troll fisheries based out of Nagasaki Prefecture (Figure 1).

Correlations among time series of SST anomalies in the three AOIs within each month were moderate to high ($\rho > 0.5$), particularly between the East China Sea and south of Shikoku AOIs, with $\rho > 0.7$ within all months between July and December. This strong spatial autocorrelation is also evident in Figure 2, with areas of high recruitment predictability covering large portions of the study region in July–October. In contrast, the temporal persistence of SST anomalies was not particularly strong in the summer and fall. Correlations between mean SST anomalies within each AOI were $< \rho = 0.5$ for any lead time of > 2 months, except for the Sea of Japan in June and July (Supplementary Figure S2). In July–December, it is therefore not possible to show precisely at which location SST was most important for recruitment. It is clear, however, that the positive relationships in fall were not a result of the temporal persistence of summer SST anomalies. For example, warmer conditions in the East China Sea in both July and December were associated with higher PBF recruitment.

Figure 2. Linear correlations between annual PBF recruitment and monthly sea surface temperatures, April to (following) January, 1982–2014. The locations of three Areas of Interest where SST was strongly correlated with recruitment are overlaid on the April map.

However, the correlation between July and December SST anomalies in this AOI across all years was only 0.12.

SST anomalies averaged across fourteen AOI/month combinations could all predict PBF recruitment with $\rho > 0.4$ (Figure 2). However, the strong spatial, and to a lesser extent temporal, autocorrelation in SST fields resulted in high multicollinearity among these indices. An hierarchical cluster analysis ("hclust" in R 3.3.2) highlighted four groups of covarying indices with cross-correlations among groups of $\rho < 0.6$. These were therefore averaged to provide spatiotemporally aggregated SST predictors of PBF recruitment. These were the Shikoku AOI averaged from June to August ("Shikoku Summer"), the East China Sea in July–August and the Sea of Japan in August–September ("Marginal Seas Summer"), the East China Sea during December ("East China Sea Winter"), and a mean of Shikoku and the East China Sea in September–October, and the Sea of Japan in October and November ("All AOIs Fall"). Warmer temperatures in all of these area/month groups resulted in significantly higher PBF recruitment ($p < 0.002$). These relationships were strongest south of Shikoku in June–August ($R^2 = 0.42$), and weakest in the East China Sea in December ($R^2 = 0.29$). ACFs at lag 1 (year) were positive for the fall and winter AOIs (0.26 and 0.18, respectively), negative for the Marginal Seas Summer AOI (-0.23), and near zero for the Shikoku Summer AOI (-0.06). However, none was statistically significant at $p < 0.05$.
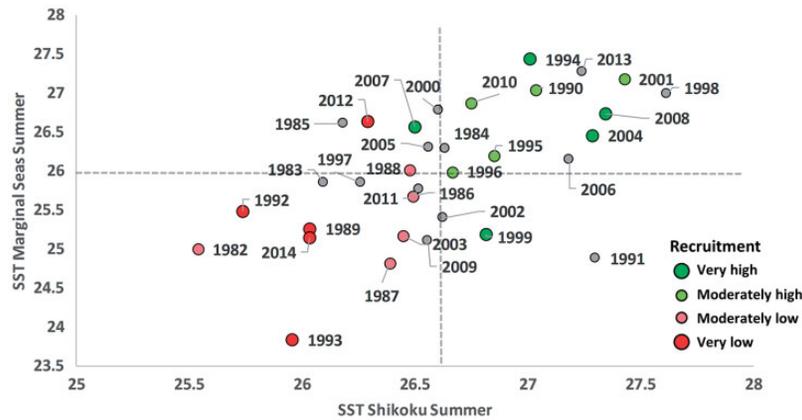
The Shikoku Summer index was most relevant to larvae spawned on the southern spawning ground, whereas the Marginal Seas Summer index was more relevant to the northern spawning ground. The 10 years of the time series with the lowest recruitment were all associated with cooler anomalies for one (e.g. 2012) or both (e.g. 1993) of these two indices (Figure 3). Conversely, the ten highest recruitment years were associated with average to warm conditions in both areas.

As SSTs during April, May and the following January were not strongly correlated with recruitment (Figure 2), we computed the PCA on SST anomalies from June to December. Approximately 65% of the variation in SST across the study area was captured by the first 5 PC axes. Mean loadings along all PCs primarily showed interannual variability, rather than any strong trend through time (Supplementary Figure S3). Correlations between PC1 and SST
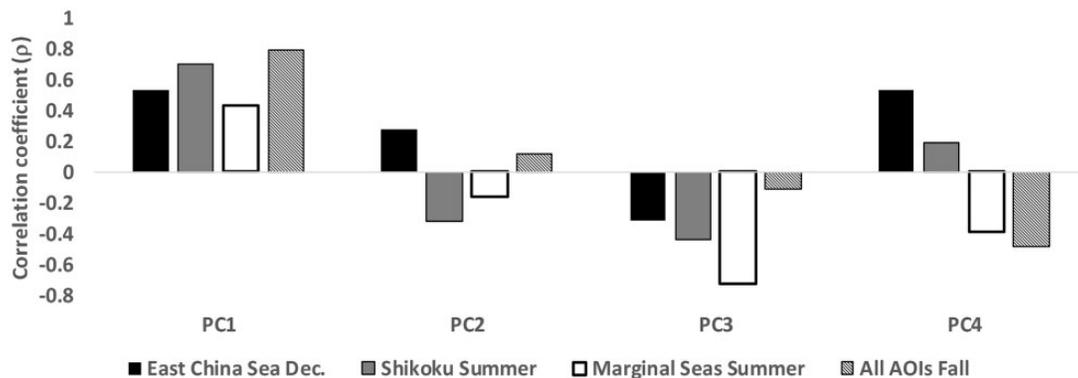
anomalies were positive for all four SST indices, suggesting that years with positive loadings along PC1 were warmer throughout the study region (Figure 4). Years with positive loading along PC2 were cooler during summer, but warmer in fall and winter, whereas years with positive loadings along PC3 were cooler in summer and fall, particularly in the marginal seas (Figure 4). PC 4 explained only 8.7% of the overall variability in SST anomalies. However, positive loadings along PC4 were associated with warmer conditions in the East China Sea during December, but cooler conditions during fall (Figure 4). Spatial correlations of each PC with SST anomalies within each month are shown for the whole study area in Supplementary Figures S4 and S5. Overall, annual values of PC1 ($\rho = 0.47$) and PC3 ($\rho = -0.52$) were more strongly correlated with annual PBF recruitment than PC5 ($\rho = 0.26$) or PCs 2 and 4 ($\rho < 0.1$).

Positive values along PC1 were associated with warmer air temperatures at 700 hPa, and negative values of the PDO and Nino 3.4 index (Table 1). In addition, positive loadings along PC2 were negatively associated with the AO, whereas values of PC3 were positively associated with the Kuroshio Current index, and the PDO. Positive values of PC4 were negatively associated with the monsoon index, and positively correlated with the Nino 3.4 index. However, whereas all these linear correlations were significant at $p < 0.05$, only the correlation between PC1 and air temperature remained so after a Bonferroni correction for multiple comparisons (Table 1).

Results shown in Table 1 suggested that both air temperature and Kuroshio Current transport could influence regional SST through local forcing. To explore this further, we calculated the correlation coefficient between June-December mean air temperature anomalies averaged across the region, and mean June–December SST anomaly at each grid point. The same exercise was then repeated to compare SST anomalies to the Kuroshio Current index. Results suggested that air temperature was a strong driver of SST anomalies, except in the Sea of Japan and east of Taiwan (Figure 5). A stronger Kuroshio Current appeared to result in weak warm SST anomalies in the southern part of the study area, and stronger cool anomalies in the eastern Sea of Japan. Correlations between area-averaged SST anomalies and area-averaged air temperature anomalies by month showed that the

Figure 3. Mean SST in the Shikoku area of interest (*x*-axis) vs. mean SST in the Marginal Seas area of interest (*y*-axis) during summer (months defined in the text). The 10 years of highest recruitment from 1982 to 2014, and the 10 years of lowest recruitment, are also shown. The grey lines represent mean SST values (1982–2014).

Figure 4. Linear correlations between each PC and SST anomalies from within the AOIs shown in Figure 2.

Table 1. Linear correlations between June and December means of four climate variables, and two local environmental variables, and mean values of each of the first four Principal Component (PC) axes, 1982–2014.

	PC1	PC2	PC3	PC4
Air temperature	0.64[a]	−0.05	−0.14	0.11
Arctic Oscillation	−0.07	−0.37*	−0.23	−0.02
Kuroshio Index	0.15	−0.01	0.50*	0.12
Monsoon Index	0.32	−0.16	−0.22	−0.44*
Nino 3.4	−0.42*	0.20	−0.11	0.43*
Pacific Decadal Oscillation	−0.45*	0.10	0.47*	0.23

*Correlations significant at $p < 0.05$.
[a]Those which remained so after a Bonferonni correction for multiple comparisons.

strongest relationships were nearly always at zero lead times (i.e. June SST anomaly was best predicted by June air temperature anomalies, rather than April or May air temperatures).
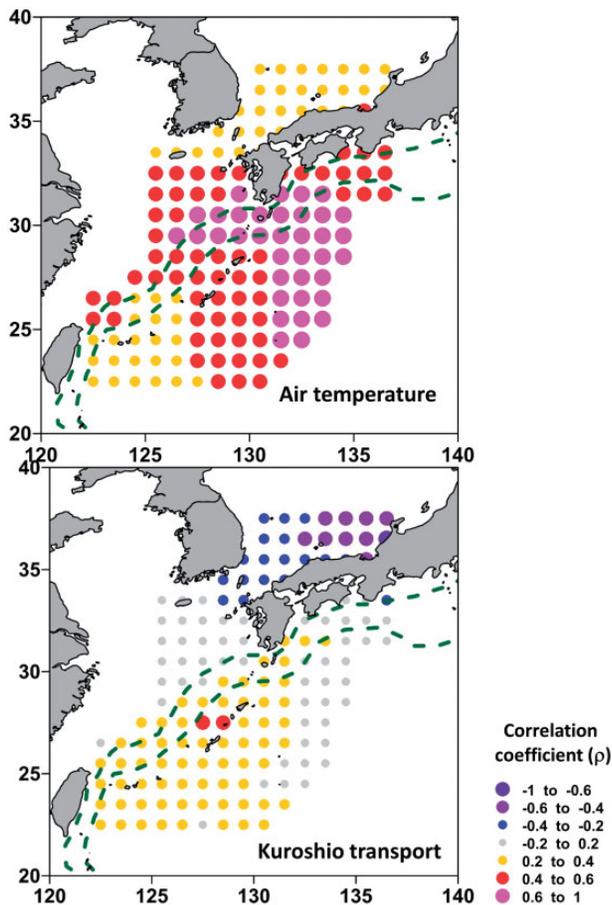
Predictive recruitment models

The first GAM ("SST GAM") was built using the four SST indices described above as predictors, along with SSB. Using $k = 3$ gave the highest R^2 (0.51), and lowest RMSE (4211.8) on the out-of-model validation data (years 2005–2014). The second GAM ("PC GAM") was built using the first five PC axes as predictors, as well as SSB. This model also showed the highest validation skill ($R^2 = 0.47$), and lowest RMSE when k was equal to 3. The final GAMs were thus built with $k = 3$.

Whereas PC1, PC3, and SSB were significant to the PC GAM at $p < 0.05$, PC2, PC4, and PC5 were not (Table 2). Excluding PC5 resulted in no loss of model skill (as determined by the −REML score and the % deviance explained by the model), but excluding PC2 and PC4 did. The final model was therefore built with all variables retained except for PC5. Similarly, excluding East China Sea December SST did not degrade the performance of the SST GAM, and so this variable was excluded from the final model (Table 2). However, excluding SSB did slightly degrade skill, and so was left in, even though the relationship was weak. Although conceptually simpler, the SST GAM performed slightly better on the out-of-model validation years ($R^2 = 0.51$ vs. $R^2 = 0.47$). The PC GAM provided a better fit to the training data ($R^2 = 0.82$ vs. $R^2 = 0.72$).

Results from the SST GAM confirmed that high PBF recruitment was associated with warm SSTs south of Shikoku and in the marginal seas during summer and fall. The partial plot for Shikoku summer SST was somewhat non-linear, however all other SST indices showed largely linear relationships with recruitment. These results corresponded closely with those from the PC

Figure 5. Spatial correlation between SST anomalies at each grid point and top: April–December mean 700 hPa air temperature anomalies across the study region, and bottom: the Kuroshio Current index, 1982–2014.

GAM, where moderately high values of PC1, low values of PC3, and high values of SSB were positively associated with recruitment (Supplementary Figure S6). Both models showed positive relationships between SSB and recruitment, although this was weaker and non-linear in the SST GAM.

While both GAMs showed that years of higher recruitment generally coincided with years of higher SSB, the relationship was inconsistent through time (Figure 6). In particular, recruitment was higher than might be expected from SSB in years after 2005. If both GAMs were re-run without SSB, the SST GAM still explained 70.3% of the deviance in recruitment for years 1982–2004 (vs. 74.7% with SSB included), and the PC GAM still explained 73.5% (vs. 81.2% with SSB included). In contrast, running a GAM with SSB as the only predictor explained 29.7%, with a positive linear relationship. This suggests that SST had a generally greater ability to explain interannual variability in recruitment than did SSB. In addition, there was no strong evidence of density dependence (which would be indicated by a consistently non-linear partial response of SSB in the GAMs). However, the PBF stock was at low biomass levels for all years between 1982 and 2015 (depletion ratios ranging from 1.8 to 9.6%: ISC, 2016), and so there may not have been enough contrast to show density dependence. The deviance in annual recruitment explained by both GAMs was quite similar, suggesting that a large portion of the

Table 2. Results of two GAMs (SST GAM and PC GAM) predicting annual PBF recruitment from surface temperatures.

Variable	*p*-Value	Model R^2		
SST GAM				
Shikoku Summer	0.007	*Training*	*Testing*	*All years*
Marginal Seas Summer	0.063	0.72	0.51	0.65
All AOIs Fall	0.073			
East China Sea December	Removed			
SSB	0.092			
PC GAM				
PC1	0.006	*Training*	*Testing*	*All years*
PC2	0.082	0.82	0.47	0.74
PC3	0.0001			
PC4	0.127			
PC5	Removed			
SSB	0.011			

SSB denotes spawning stock biomass from the most recent stock assessment model. The R^2 for each model is shown for the training dataset (1982–2004), the out-of-model testing dataset (2005–2014), and for all years together.

temperature effect was associated with the AOIs defined in Figure 2. However, the PC GAM did noticeably better at several points in the time series, particularly the recruitment peaks in 1994 and 2004 (Figure 6). Both GAMs were able to replicate the overall lower levels of recruitment in the 1980s, with higher values since 1994, but both models over-predicted in the last 3 years of the time series, particularly during 2013 (Figure 6).
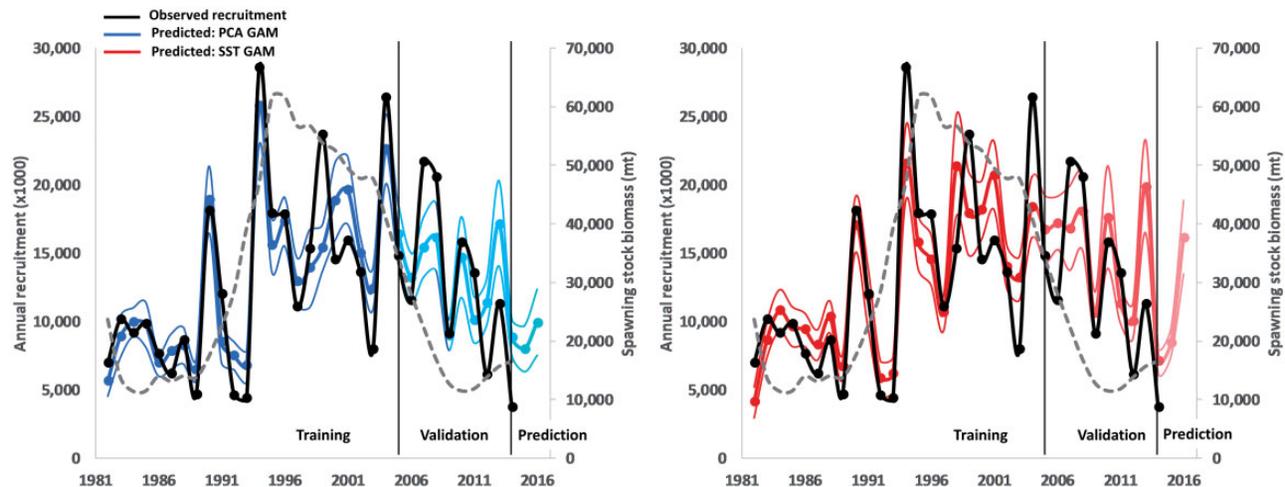
When the two GAMs were applied to OISST fields from 2015 and 2016 (with SSB kept at 2014 levels), both models predicted that recruitment in 2015 would be similar to what it was in 2014, and 2016 recruitment would be more favourable. The SST GAM was considerably more optimistic than the PC GAM, however. In both years, SST in the AOIs shown in Figure 2 was at least >0.5°C above normal in 2016. In contrast, temperatures in the marginal seas during summer in 2015 were >1.0°C cooler than average. Higher predicted recruitment in 2016 was therefore a result of warm anomalies across the region in summer to fall, whereas 2015 had a cool summer and fall, resulting in predictions of below average recruitment.

Discussion
Temperature effects on PBF recruitment
Results from this study suggest a spatially and temporally variable temperature effect on interannual PBF recruitment. The effect was most marked off the Pacific coast of Shikoku, in the northern East China Sea and in the southwest Sea of Japan. The strongest year classes were associated with warm conditions from summer to early winter, in all AOIs. The highest correlations were present south of Shikoku, a nursery area for small juveniles advected northwards in the Kuroshio Current from the southern spawning ground (Kitagawa *et al.*, 2010). PBF arriving off Shikoku in June– August occupy warm waters (mixed layer > 27°C) during their first summer (Furukawa *et al.*, 2017), and remain in the area through winter before migrating northwards the following spring.

In contrast, the Sea of Japan in August and September is primarily larval and juvenile habitat for the northern spawning ground. Cooling temperatures in the Sea of Japan during fall result in southward migration of juvenile PBF towards Tsushima Island and the East China Sea (Kitagawa *et al.*, 2006). By fall,

Figure 6. Time series of observed and predicted PBF recruitment from both GAMs (left: PCA GAM, right: SST GAM), with spawning stock biomass also shown. Standard errors are shown in thin lines for each GAM. Vertical lines divide the time series into years used for GAM training (1982–2004), validation (2005–2014), and predictions of 2015 and 2016 recruitment using OISST fields, and 2014 levels of SSB.

small juveniles from both spawning grounds mix in the East China Sea area (Fujioka *et al.*, 2016), and so correlations between SST and recruitment in the combined marginal seas region are not specific to either one of the two spawning grounds. Some juveniles from the southern spawning ground arrive in the East China Sea as early as July, around the same time as spawning commences in the Sea of Japan. The positive effect of temperature on recruitment in the marginal seas in summer could therefore apply primarily to larvae in the Sea of Japan, to juveniles in the East China Sea, or both.

In contrast, there were no strong correlations observed between recruitment and temperature near Taiwan and the southern Nansei Islands in April and May, with some weak positive correlations in June. This suggests that, for the southern spawning ground, temperature-driven survival of larval PBF is not driving recruitment variability. Recent studies suggest that PBF survival to the juvenile phase may depend primarily on growth-dependent survival of larvae (Tanaka *et al.*, 2006, 2014; Satoh *et al.*, 2013; Watai *et al.*, 2017). Whereas studies on cultured PBF larvae growth show strong positive relationships with temperature (Kimura *et al.*, 2010), results have been more complex for field collected larvae. Satoh *et al.* (2013, 2014) showed that temperature and prey density interacted to positively influenced PBF larval growth. Conversely, Tanaka *et al.* (2006) found little effect of temperature on larval PBF growth, across a range of ~25–29°C. At <14 days post hatch, PBF larvae are primarily zooplanktivorous (Tanaka *et al.*, 2014). Tanaka *et al.* (2008) showed that larval PBF have a very low tolerance to starvation, and so prey densities may be more important for determining survival than temperature for larvae spawned on the warmer southern spawning ground.

Mortality rates on pelagic early life stages of fishes are often assumed to be highest at younger ages, with recruitment strength determined by high and variable mortality at the larval stage (Bailey and Houde, 1989; Pepin and Myers, 1991). However, studies on captive PBF have demonstrated that mortality on small juveniles can also be substantial. This is often associated with stress from handling, transfer, and collisions with tank edges, but Tsuda *et al.* (2012) also showed a temperature effect on 5–6 month old juvenile PBF in sea cages. Decreases in ambient

water temperature below ~20°C resulted in decreased daily survival, with cooling below 15–17°C causing particularly strong spikes in mortality. Colder temperatures in juvenile PBF habitats over their first year of life, before they are completely endothermic (Kubo *et al.*, 2008), may therefore result in higher mortality, particularly during fall and winter. Steady and fast growth in early larval phases, whether mediated by temperature or prey availability, may determine the likelihood of survival to the juvenile stage, but overall recruitment of age-0 fish may also depend on temperature-driven survival in juveniles. Direct mortality from cold temperatures is most likely to occur in late fall and winter, however unfavourable temperatures may also decrease survival through indirect mechanisms (e.g. Ottersen and Loeng, 2000). These may include slower juvenile growth causing higher predation mortality, or temperature-driven impacts on prey fields. Such complex regulation of recruitment by differing processes over multiple life stages has been shown previously for some species, which are benthic as juveniles and adults (e.g. Duffy-Anderson *et al.*, 2005), but not for pelagic species such as tunas.

Another possibility is that temperature is influencing the accessibility of age-0 fish to troll fisheries, and thus the recruitment index. Unlike the captive PBF studied by Tsuda *et al.* (2012), wild juveniles can move away from unsuitable thermal habitat. Mean SST near to the main troll fishing grounds in Nagasaki Prefecture begins to cool below 20°C in December, and may fall below 16°C from January to April (Ichinokawa *et al.*, 2014; this study). Most fishing vessels targeting age-0 PBF have limited range, and so temperature-driven southward movement of age-0 PBF towards the Kuroshio Current boundary (Kitagawa *et al.*, 2006), could result in less fish being available to the troll fisheries working in the Tsushima Strait. This could bias the recruitment index derived from catches in these fisheries. Alternatively, cooler temperatures could lead to slower growth and smaller sizes in age-0 juveniles, reducing their vulnerability to gears employed by the troll fishery. Examination of both of these possibilities in future studies would provide more information on the representativeness of the current troll-based recruitment index, and help to better define mechanistic links between temperature and recruitment strength.

Climate drivers of variability in larval habitats

Our results showed that SST had strong predictive skill for PBF recruitment, and so the underlying drivers of ocean temperature variability in the region are important to understand. SST within the AOIs varied widely across the 33 years of data. For example, three of the four SST indices varied by $>2°C$ interannually, and the Sea of Japan during August varied by $> 5°C$. PCA of the SST fields suggested that dynamics in the Sea of Japan were often distinct from those in the open Pacific, or in the southern East China Sea, especially in June and July. While the importance of the Kuroshio Current and associated eddies to PBF recruitment has been highlighted previously (Kimura *et al.*, 2010; Kitagawa *et al.*, 2010), the strong SST variability shown in this study was mostly atmospheric in origin.

Years, which were warmer across most of the study region (and thus loaded positively along PC1), were associated with above average air temperatures, and negative values of ENSO and the PDO. PC3 appeared to incorporate some of the variability from the PDO, and Kuroshio Current flow, whereas PC4 had some relation to the monsoon index, and ENSO. El Niño events result in negative SST anomalies in the western North Pacific, as atmospheric teleconnections drive changes in air temperatures, wind patterns, and humidity (Alexander *et al.*, 2002, 2004), and so their link to regional SST variability is expected. The correlation between area-averaged SST anomalies and a June–December mean of the Nino 3.4 index was stronger than that between mean 700 hPa air temperature anomalies and the same Nino 3.4 index ($\rho = -0.44$ vs. $\rho = -0.21$). This appears to confirm the importance of variables other than air temperature in linking ENSO to SST anomalies, such as cloud cover (Alexander *et al.*, 2004).

While air temperature explained more of the variability in SST than did Kuroshio Current flow, a stronger Kuroshio Current was associated with positive SST anomalies near to the Nansei Islands, and negative anomalies in the southern Sea of Japan. As the Kuroshio strengthens, its path meanders less in the East China Sea, and the Tsushima Current (which transports warm water northwards through the Tsushima Strait) weakens. This leads to negative temperature anomalies in the southwest Sea of Japan (Gordon and Giulivi, 2004).

While positive phases of the PDO are associated with negative SST anomalies near to Japan, the mechanisms vary seasonally (Newman *et al.*, 2016). Winter temperature anomalies can become decoupled from the surface as the water column stratifies during summer. These anomalies may then "reemerge" as stratification breaks down the following fall, leading to time series of winter SST that are correlated year-to-year, lengthening the overall timescale of SST anomalies (Alexander *et al.*, 1999). In contrast, warm season SST anomalies in the North Pacific are primarily related to air–sea heat fluxes, and local forcing (Newman *et al.*, 2016). Some studies have linked the strength of the Kuroshio Current south of Japan to the PDO at zero lag (e.g. Gordon and Giulivi, 2004; Andres *et al.*, 2009). However, Soeyanto *et al.* (2014) found that the correlation described by Andres *et al.* (2009) weakened substantially when extended to 2012. The correlations between the PDO and PBF recruitment noted previously (Sakuramoto, 2016; Harford *et al.*, 2017; Ishida *et al.*, 2018) thus appear likely to result from connections between the PDO and local SST anomalies. The higher correlations between the PDO and recruitment in fall noted by Harford *et al.* (2017) and Ishida *et al.* (2018) likely result from the stronger effect of the PDO on regional SSTs during the cooler months, rather than a stronger effect of environmental variability on recruitment during fall. As shown in this study, temperature effects on recruitment are also likely to be present during summer, but SST during this season is not as well described by the PDO.

Management implications

SST anomalies in the marginal seas vs. those in the open Pacific did not always correspond strongly in space and time, with the result that conditions could be potentially favourable in some months and locations, but not others. Itoh (2009) used daily otolith increments to show comparatively high contribution of the Sea of Japan spawning ground to recruitment in 1994, low contribution in 1993, and moderate contribution in 1995–1997. This is consistent with the marginal seas being warm in 1994, cold in 1993, and moderate in 1995–1997 during summer, as shown in the present study (Figure 3). As smaller adults spawn in the Sea of Japan, and larger fish further south towards Taiwan (Itoh, 2006), this could result in substantial interannual variability in reproductive output by both spawning ground, and by adult size class. Although the current recruitment index is spatially aggregated, future work could consider estimating recruitment by spawning ground, by expanding work that assigns juveniles to spawning ground based on back-calculated hatch dates. This would enhance understanding of how environmental conditions, including temperature, drive variability in recruitment from each of the two spawning grounds.

The current stock assessment model for PBF assumes that SSB does not drive substantial variation in recruitment, but there has been significant discussion around this point (e.g. ISC, 2016; Nakatsuka *et al.*, 2017). The importance of SSB to the predictive GAMs was relatively weak compared with the effects of SST, with both models retaining much of their skill if SSB was removed. The relationship between SSB and recruitment was nonstationary, even if we followed Nakatsuka *et al.* (2017), and used a 5-year moving mean of both variables (results not shown). The SRR for PBF may therefore not be well represented by traditional models, and environmental effects may be substantially confounding it, a situation likely common to many fish stocks (e.g. Szuwalski *et al.*, 2015; Lowerre-Barbieri *et al.*, 2017). Future work could test the development of an environmentally explicit SRR model, where the potential influence of environmental on density-dependence could be included. However, the mechanistic processes linking SSB and environment to recruitment require further investigation. Temperature-driven changes in survival, growth, or distribution of early life stages are all plausible, and should be examined more closely using field and laboratory studies.

In response to increasing concern about the status of the PBF stock, the Western and Central Pacific Fisheries Commission (WCPFC) recommended the adoption of an emergency rule in the event of "drastic drops in recruitment" (WCPFC, 2015). While the specifics of this rule are still under development, the relationship between SST and recruitment highlighted in this study could contribute to this type of measure, with anomalously cold SSTs providing an early warning to managers that recruitment may be low in that year. This can potentially be incorporated into a more formal decision rule, which could increase the adaptive management potential for the stock. However, the potential benefit of such a rule to the long-term sustainability of the stock, its

rebuilding potential, and future harvest would need to be quantitatively assessed through a management strategy evaluation, before inclusion in the formal management process. Alternatively, if future research can show that SST is significantly influencing availability of age-0 fish to the troll fisheries whose catches form the basis of the recruitment index, a temperature-based standardization could be explored.

The strong relationship between PBF recruitment and SST also raises the possibility of future prediction capabilities, either on a seasonal or multi-annual time scale (Tommasi *et al.*, 2017b). However, whereas seasonal prediction of SST anomalies in the Sea of Japan region is strong at a 6–12 month lead time in winter and spring, prediction of summer SST anomalies is only moderate (Stock *et al.*, 2015). Multiyear prediction skill of annual SST upper and lower terciles for the Sea of Japan and Pacific coastal Japan is relatively strong up to 10 years in advance (Tommasi *et al.*, 2017c). However, predictive capabilities during summer and at the smaller spatial scale relevant to PBF recruitment may be lower due to the inability of current prediction systems to represent fine scale shelf processes and the stronger importance of local atmospheric variability, rather than predictable basin-scale SST variations, in modulating summer SST. This presents a challenge for the seasonal–decadal prediction of PBF recruitment with current models.

On longer timescales, climate change is likely to drive substantial warming on PBF spawning grounds in the coming decades. The southern PBF spawning area is projected to increase in temperature by 1.5–2°C by the end of the 21st century, while the Sea of Japan may warm by more than 3°C (Woodworth-Jefcoats *et al.*, 2017). This warming may benefit PBF recruitment, if we assume that the relationships defined in this study continue to hold. However, increasing incidence of very warm (>29°C) temperatures may be deleterious. Kimura *et al.* (2007) showed that increasing ambient temperature from 26 to 29°C over a short period of time resulted in increased mortality in cultured PBF larvae. In the field, this temperature increase would happen over a much longer time scale, and may allow some adaptation to new conditions. Nevertheless, the emergence of conditions outside the range of historical measurements, in terms of temperature, regional current systems, prey fields, metabolic demands, and other variables, may challenge the adaptation of PBF across life stages. Kimura *et al.* (2010) highlighted the seemingly delicate balance between SSTs on the southern spawning ground, transport of larvae northwards in the Kuroshio Current, and arrival of post-larvae on nursery grounds around coastal Japan. The projected strengthening of the Kuroshio Current (Sakamoto *et al.*, 2005), and the different warming rates projected for the two spawning grounds may require complex adaptation responses, on a relatively short evolutionary timescale. How long-term climate change will impact PBF is thus complex, and difficult to predict.

Conclusions

Results from this study highlighted strong correlations between spatiotemporal variability of spring—early winter SSTs around coastal Japan, and annual PBF recruitment. Warmer temperatures appeared to be most advantageous, with near linear positive relationships in most cases. Interannual variability in SSTs was most strongly associated with air temperature anomalies, with some weaker connections to the ENSO cycle, the PDO, and Kuroshio Current transport. Predictive models for recruitment using the main modes of SSTs variability may allow more adaptive management of PBF, across environmental regime shifts, and under future climate change conditions.

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

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