

Decadal decline in demersal fish biomass coincident with a prolonged drought and the introduction of an exotic starfish

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ABSTRACT: Between 1990 and 2011, Port Phillip Bay in southern Australia experienced 2 major ecological disturbances: a prolonged drought from 1997 to 2010, and the introduction of the invasive starfish, *Asterias amurensis*. The drought reduced land-based nitrogen inputs by 64%, and the biomass of *A. amurensis* in the deep centre of the bay peaked at 56% of the resident fish biomass in 2000. The impacts of these disturbances on fish were assessed using a demersal trawl time-series spanning 2 decades (1990 to 2011). The timing and spatial extent of changes to fish biomass were analysed using ANCOVA and change point analysis. During the drought, fish biomass declined by 69% in the deep centre of the bay, by 50% at intermediate depths, and showed no significant change around the shallow fringes. This spatial pattern is consistent with hydrodynamic modelling, which suggests that during the drought a greater proportion of the (lower) nitrogen input was retained near the coastal fringe. Most of the decline in fish biomass was attributed to the cumulative effects of reduced productivity during the 12 yr drought. However, declines in 3 species in the deep region were attributed to competition with *A. amurensis*. Each of these species exhibited high dietary overlap with *A. amurensis* and displayed sharp declines in biomass coinciding with the peak abundance of *A. amurensis* in 2000.

KEY WORDS: Nutrient · Drought · *Asterias* · Exotic species · Trawl time-series · Port Phillip Bay

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INTRODUCTION

Long-term ecological studies provide many key insights indispensable to natural resource management. These include quantifying ecological responses to drivers of ecological change, understanding complex ecological processes, providing core data to develop and test ecological models, providing platforms for collaborative studies and providing data at scales relevant to management (Lindenmayer et al. 2012). Long-term fishery-independent demersal trawl surveys provide a key source of information about the productivity (Overholtz & Tyler 1985, Bailey et al. 2009) and trophic structure (Pinnegar et al.

2002, Heath 2005) of demersal fish assemblages. Where long time-series exist, trawl surveys have been pivotal in distinguishing short- (Anderson & Piatt 1999, Erzini et al. 2005) and long-term (Beare et al. 2004, ter Hofstede et al. 2010) climatic variability from the direct effects of fishing on demersal fish assemblages. Trawl time-series have documented latitudinal changes in species ranges (Heessen 1996, Beare et al. 2004, ter Hofstede et al. 2010), cyclical changes in productivity (Anderson & Piatt 1999) and long-term declines in targeted fish species (Bailey et al. 2009). In coastal areas, long-term trawl time-series have also identified changes in fish assemblages linked to reductions in freshwater flows resulting

from greater demands for water upstream (Thomson et al. 2010).

Between 1990 and 2011, Port Phillip Bay in southern Australia experienced 2 major ecological disturbances that affected the input and dispersal of nutrients as well as the way production was distributed between different biological components within the bay. First, southern Australia experienced the longest and most severe drought on record from 1997 to mid-2010 (Ummenhofer et al. 2009). Rainfall declined by 18% across Victoria, leading to reductions in river flows and significant reductions in nutrient loads into the bay. Secondly, the exotic starfish *Asterias amurensis* was introduced into Port Phillip Bay in 1995, and by 2000 its biomass peaked at 2800 t (165 million starfish)—most of this in the deep central region of the bay (Parry et al. 2004). *A. amurensis* is native to the northwest Pacific, and is a voracious predator that has had a major impact on bivalve populations in southeastern Tasmania (Ross et al. 2002, 2003a,b, 2004) and throughout its native range in Japan (Byrne et al. 2013).

The drought was expected to gradually reduce both productivity and fish biomass (Loneragan & Bunn 1999). The link between nutrients and fish production is clear in areas of upwelling, where 50% of fish production occurs in 0.1% of the (nutrient rich) ocean (Ryther 1969), and collapses of fish populations are common when upwelling ceases (Barber & Chavez 1983). Where upwelling does not occur, changes in nutrient inputs would be expected to have more subtle effects on fish abundance. Such effects are not well documented, although correlations between annual flows in coastal rivers and the size of fish catches (e.g. Livingston et al. 1997, Grimes 2001, Lloret et al. 2001, Quiñones & Montes 2001) provide indirect evidence for such an effect. The mechanisms underlying these correlations remain uncertain (Loneragan & Bunn 1999, Gillanders & Kingsford 2002, Connolly et al. 2009), but a review by Gillson et al. (2009) identified 5 possible mechanisms. The most applicable of these to non-estuarine marine embayments, such as Port Phillip Bay, is that decreases in nutrient supply decrease primary and secondary production, leading to reduced fish biomass through lower recruitment or growth, or through increased mortality and emigration of adults.

During the drought, reductions in fish biomass were expected to be greatest in regions of the bay subject to the largest decrease in nutrient supply, which were identified from changes in circulation patterns obtained from available hydrodynamic

modelling. If competition with *A. amurensis* was important, sharp rather than gradual declines in fish biomass were expected. These declines were expected to be greatest in the deep region of the bay where *A. amurensis* was most abundant, and to occur in 2000 when the *A. amurensis* biomass peaked (Parry et al. 2004). Declines in fish biomass due to competition for food were also only expected for species with a high dietary overlap with *A. amurensis*.

The present study examined the impact of these disturbances using a demersal trawl time-series, where the same 20 stations were sampled annually over 2 decades (1990 to 2011). As the timing of the drought and the arrival and expansion of *A. amurensis* overlapped, separating the impacts of the drought and the exotic invasion was challenging. Regression analysis and ANCOVA were used to detect differences between rates of change in 3 depth-related regions (shallow, intermediate and deep) of the bay during the drought. Change point analysis was used to objectively determine the timing and regions where sharp changes in fish abundance occurred, as these may be indicative of competition with starfish. We examined spatial changes observed in total fish biomass, biomass of 2 functional feeding groups and 8 abundant species to determine the factors most likely to have caused the changes for each grouping and species.

MATERIALS AND METHODS

Study location

Port Phillip Bay is a large coastal embayment (2000 km²) with a coastline approximately 264 km in length and a narrow entrance (~3 km wide) that restricts tidal exchange with central Bass Strait (Fig. 1), an oligotrophic region with no major rivers or upwelling (Gibbs et al. 1986). Half of Port Phillip Bay is <8 m deep and its maximum depth is 24 m. The bay is dominated by a central deep basin adjacent to a shallow western arm (Fig. 1). A tidal delta ('The Great Sands') forms an extensive region of shallow sand banks that stretch across the bay's entrance, attenuating both oceanic waves and tides. The sediments of Port Phillip Bay are a mixture of fine sand and silt, with coarser sediments in shallow areas and fine sediments dominating the central deeper basin (Harris et al. 1996). More than 4 million people live in the catchments, most of them in the city of Melbourne at the northern end of the bay (Fig. 1). Recreational fishing occurs throughout the bay; there is a

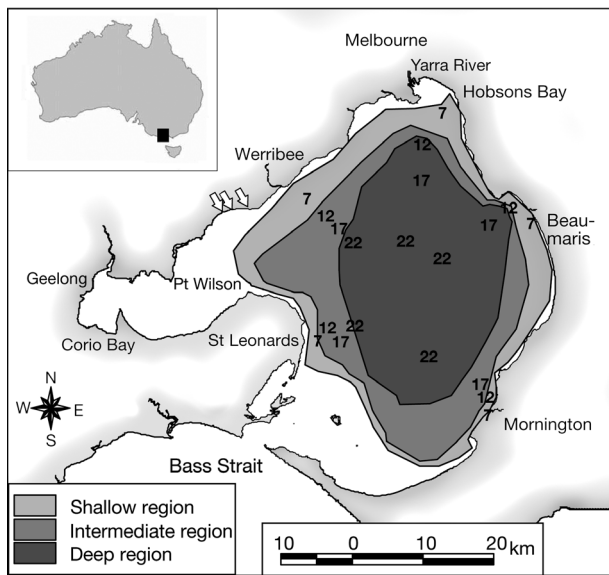


Fig. 1. Port Phillip Bay, showing the location of fixed trawl stations at 7, 12, 17 and 22 m depths along Beaumaris, Hobsons Bay, Mornington, St. Leonards and Werribee transects. Arrows indicate the 3 main inputs from the Western Treatment Plant. Inset: location of Port Phillip Bay on the Australian coast

small amount of commercial fishing with handlines, longlines, purse seines, beach seines and mesh nets, but commercial trawling has never been permitted in Port Phillip Bay.

The Yarra River flows into the north of the bay (Fig. 1) and supplies more than 70% of freshwater and 40 to 50% of the nitrogen inputs from its catchment (Harris et al. 1996). Only 15% of the catchment area is urbanised, although there is significant urban runoff of nutrients, suspended sediments and some heavy metals. The largest source of nutrients into Port Phillip Bay is from Melbourne Water's Western Treatment Plant (WTP) at Werribee (Fig. 1), where tertiary treated sewage effluent containing high loads of nitrogen and phosphorus is discharged. Emphasis has been placed on the role of nitrogen rather than phosphorus in this study, as nitrogen is considered the key limiting nutrient for primary producers in Port Phillip Bay (Harris et al. 1996). In the mid-1990s, the WTP was estimated to contribute >50% of all nitrogen inputs into Port Phillip Bay (Harris et al. 1996), although its contribution has declined since 2001 following improved sewage treatment. Reductions in nitrogen input during the drought (1997 to mid-2010) were exacerbated by reductions in the discharge of nitrogen from the WTP. After 1997, drought-related low flow conditions

increased the nitrogen removal efficiency of the WTP, and between 2001 and 2005, upgraded sewage treatment further reduced the amount of nitrogen in the WTP discharge.

Field methods

Demersal fish assemblages were sampled annually using a demersal trawl net at 20 stations stratified by depth in Port Phillip Bay (Fig. 1) from 1990 to 2011. Stations were sampled during March (late February in 1994, and early April in 1993 and 1997), in all years except 1998 and 2001. Stations were located along 5 transects running perpendicular to the coast at depths of 7, 12, 17 and 22 m (Fig. 1). At each station, two 5 min tows were undertaken with a demersal trawl net (13 m wide \times 2.2 m high, with a mean door spread of 38 m, but this varied with depth) towed over a distance of ~500 m. The length of the tow cable used at each depth was standardised so that 50 m of tow cable was used at 7 and 12 m depth, 75 m at 17 m depth and 100 m at 22 m depth. The duration of each tow (nominally 5 min) was measured from the time that load cell clamps were attached until the winch commenced the retrieval of the net. The speed of the net across the benthos (2.7 to 3.3 knots) was estimated from the tow duration and GPS vessel positions at the start and finish of each tow. During 2003 and 2004, the wrong tow cable length was used at the 7 m stations, and therefore data from these years were excluded from the analysis. Upon retrieval of the net, fish and invertebrates were sorted on deck and the number and total (wet) mass of each species was recorded. Substantial overlap in personnel ensured consistent sampling methodologies and fish identification over the course of the study.

Correction for changes in vessel and net efficiency

Three vessels were used during the study. Between 1990 and 1997, sampling was undertaken using a 20 m research vessel, and from 1999 to 2011, 2 commercial trawlers of similar dimensions were used. The effect of change in vessels on catches was minimised by selecting vessels of similar size and using the same skipper from 1990 to 2000, and as an onboard advisor on subsequent trawls.

A total of 6 trawl nets were used during the study. Two nets were used before 2000, when new nets of the same design were introduced progressively as nets became worn. One new net was introduced in

2000, 2003, 2007 and 2011. From 1999 onwards, vessels had 2 net drums enabling different nets to be towed at the same site, with the catch of each new net compared with that of an existing net. This ensured that temporal trends were not the result of changes in net efficiency. Where differences in fishing efficiency were detected, alterations were made to the new net. Occasionally, corrections to catches were required due to differences between nets, as described in Parry et al. (2009).

Data analysis

Spatial analysis of fish communities

Stations were split into 3 regional groups based on Bray-Curtis similarity of fish communities and non-metric multidimensional scaling, as described in Parry et al. (1995). The 3 regional groups showed similar spatial differences to those seen in sediment type and infauna (Currie & Parry 1999) and epifauna (Cohen et al. 2000). The 3 groups, designated as 'regions' in this study, comprised 5 stations at the 7 m depth (shallow region), 7 stations primarily at 12 and 17 m depths (intermediate region) and 8 stations primarily at the 22 m depth (deep region) (Fig. 1). Stations in the deep region were characterised by finer, siltier sediments than stations grouped in the intermediate region, whilst stations in the shallow region were dominated by coarser sediments (fine sands) (Harris et al. 1996).

Spatio-temporal analysis of changes in fish biomass tow^{-1}

Rates of change in fish biomass tow^{-1} for each region of the bay were analysed for the period of the

drought. Based on annual meteorological records, the drought lasted from 1997 to 2009; however, rainfall did not increase until after the trawl sampling in March 2010, thus the 2010 trawling was included within the period of drought. For the period 1997 to 2010, regression analysis was used to estimate the slope and significance of $\log_{10}(\text{biomass } \text{tow}^{-1})$ versus year, and analysis of covariance was used to compare the slopes of these regression lines between shallow, intermediate and deep regions for total biomass (all 113 species), 2 functional feeding groups (obligate benthic feeders [OBF] and mixed feeders) and 8 of the 11 most common fish species. Regressions showing significant autocorrelation based on the Durbin-Watson test were corrected by fitting an AR(1) term using the Yule-Walker method in Proc Autoreg in SAS® 9.3. This correction was applied to 8 of the 33 regression analyses, but the correction only marginally affected slopes and significance levels.

There were 26 pelagic species (which contributed only 2% of the total fish biomass), 71 species of OBF and 16 species of mixed feeders. OBF are species that feed only on the benthos, whereas mixed feeders can switch between benthic and pelagic prey depending on their availability. Fish species were assigned to functional feeding groups using dietary information in Parry et al. (1995) (Table 1). The 8 species chosen for individual analysis were eagle ray *Myliobatis tenuicaudatus*, eastern shovelnose stingaree *Trygonoptera imitata*, globefish *Diodon nichthemerus*, sand flathead *Platycephalus bassensis*, southern fiddler ray *Trygonorrhina dumerilli*, sparsely spotted stingaree *Urolophus paucimaculatus*, spiny gurnard *Lepidotrigla papilio* and yank flathead *Platycephalus speculator*. Three species with high biomass (snapper *Chrysophrys auratus*, red mullet *Upeneichthys vlamingii* and smooth stingray *Dasyatis brevicaudata*) were not analysed individually. Snapper were excluded as the trawl net caught predominantly the

Table 1. Diets of common fish species in Port Phillip Bay (from Parry et al. 1995), indicating functional feeding groups assigned. OBF: obligate benthic feeders; mixed feeders: fish that feed on benthic and pelagic prey

Species	Diet (in order of importance)	Feeding group
Eagle ray	Small decapods, molluscs, ascidians	OBF
Eastern shovelnose stingaree	Polychaetes	OBF
Globefish	Molluscs, small decapods, echinocardium	OBF
Southern fiddler	Decapods, flathead and other small fish, cephalopods	OBF ^a
Sparsely spotted stingaree	Small decapods, amphipods	OBF
Spiny gurnard	Amphipods, isopods, small decapods	OBF
Sand flathead	Decapods, small benthic fish, anchovies	Mixed feeders
Yank flathead	Small fish	Mixed feeders

^aParry et al. (1995) reported 5% pelagic taxa in diet

1+ age class, so trends in catches primarily reflected trends in recruitment. Catches of the other 2 species exhibited high variances as smooth stingray are very large but rarely caught, and red mullet form schools. The 8 chosen species accounted for 83% of the total fish biomass caught between 1990 and 2011.

Change point analysis

Two methods were chosen to identify possible change points for the period of 1990 to 2011. Bayesian change point (bcp) analysis and sequential *t*-test analysis of regime shifts (STARS) were used to explore temporal and spatial patterns in $\log_{10}(\text{biomass} / \text{tow} + 0.1)$ for the same categories used in the ANCOVA: total fish biomass, 2 functional feeding groups and 8 common species. Both methods are able to identify multiple change points in a time-series; bcp was chosen as, unlike other methods, it estimates the probability of a change point at each location and so provides a summary reflecting the degree of uncertainty of change points. The STARS method was chosen as it is less sensitive to temporal trends than other methods (Rodionov 2004). However, all of the methods available to detect step changes in the mean of a time-series (Rodionov 2005) assume that there is a step change rather than a trend in the mean. This assumption is often violated in time-series of natural systems; where there is a temporal trend, change point analysis will often incorrectly identify a step change (or changes) in the middle of the trend (Rodionov 2004, Möllmann & Diekmann 2012).

Bayesian change point analyses were obtained using the 'bcp' package in R (Erdman & Emerson 2007), which estimates the posterior probability of a change point for each year, indicating the likelihood that a change point occurred following that year. The bcp analysis is an implementation of Barry & Hartigan's (1993) product partition model for change point analysis using Markov Chain Monte Carlo methods. A burn-in run of 50 000 iterations was performed, and 50 000 iterations were used to sample the posterior distribution. Convergence diagnostics were performed using the R 'coda' package (Plummer et al. 2009), and convergence was tested using the methods of Geweke (1992) and Heidelberger & Welch (1983). As there were missing data in 1998 and 2001, and a strong change point for many taxa in 2000, sensitivity analysis was undertaken to ensure this change point was not an artefact of the missing data. Change point analysis was re-run using estimates for

catches in 1998 and 2000, based on the mean catches in 1997–1999 and 2000–2002, respectively.

STARS analysis was undertaken using software made available by the method's author (www.bering-climate.noaa.gov/regimes/). The algorithm that was used assumed a cut-off length of 8 yr and a probability level of $p < 0.05$.

Environmental trends

Information on environmental trends in Port Phillip Bay from 1985 to 2011 was obtained from several sources. Yarra River flow records were obtained from measurements at 3 gauging stations monitored by Melbourne Water. Daily flows from gauging stations on each of the 3 main tributaries (Maribyrnong River at Keilor, Yarra River at Chandler Highway and Moonee Ponds Creek at St. Georges Road) were summed. Salinity records were sourced from a long-term water quality monitoring program in central Port Phillip Bay (EPA Monitoring Site ID No. 1229), which was sampled approximately monthly by the Victorian Environment Protection Authority (EPA). WTP nitrogen loads into Port Phillip Bay were calculated from daily flow and weekly nutrient concentrations at each discharge outlet, supplied by Melbourne Water. Catchment loads of nitrogen into Port Phillip Bay were obtained from the PortsE2 WaterCAST catchment model. This model used hourly or daily runoff estimates from 2 rainfall runoff models (AWBM and SIMHYD), and these models in turn included hydrological data from 14 catchments and 17 land use types (Stewart 2012). During the drought, the percent change in nitrogen loads into Port Phillip Bay from the WTP, the catchment and their total were estimated by comparing mean N loads in 1995–1996 and 2008–2009.

Hourly wind records for the period 1992 to 2009 were obtained from the Bureau of Meteorology's Pt. Wilson automated weather station. This station provides the most extensive record of wind speed and direction available for the bay, but record-keeping did not commence until 1992. Missing hourly records (7.3%) were estimated (D. Greer pers. comm.) using predicted wind speeds from NOAA's NCEP Climate Forecast System Reanalysis (CFSR) Hourly Time-Series Product. Predicted wind speeds and directions were compared with measurements at Pt. Wilson, and a regression between predicted and measured values was used to fill gaps in the wind record.

Annual estimates of the total demersal fish biomass in each region of Port Phillip Bay (i.e. shallow, inter-

Table 2. Comparison of slopes of \log_{10} (mean biomass tow^{-1}) vs. year for 3 regions (shallow, intermediate and deep) of Port Phillip Bay during the drought for total fish biomass and 2 trophic groups (obligate benthic feeders [OBF] and mixed feeders), as well as 8 individual species. The significance of the slope is shown (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$), as is the significant differences in slopes between regions (= : $p > 0.05$, < or > : $p < 0.05$, >> : $p < 0.01$, >>> : $p < 0.001$), the percentage change in fish abundance between 1997 and 2009, and the dietary overlap between *Asterias amurensis* and fish species

Group/ species	Slope of \log_{10} (Mean catch tow^{-1} , kg) vs. year, 1997–2010		Significance of differences between slopes	% change in biomass 1997–2010 ^a		Dietary overlap with <i>A. amurensis</i>	% change in biomass 2010–2011			
	Shallow	Intermediate		Deep	Shallow		Intermediate	Deep		
Total biomass	0.005	-0.024*	-0.044***	S >>> I >>> D (S >>>> D)	35	-50	-69	110	47	102
OBF	0.006	-0.011	-0.042*	S >>> I >>> D	38	-12	-65	75	40	38
Mixed feeders	-0.004	-0.058**	-0.045***	S = I = D (S >> D)	19	-87	-73	446	85	119
Obligate benthic feeders										
Species with step change point in 2000 in deep region										
Eagle ray	0.002	0.018	-0.064	S = I > D (S = D)	-30	286	-78	+++ ^b	-48	79
Eastern shovelnose stingaree	0.028*	-0.011	-0.031	S = I >>> D (S >>>> D)	54	-39	-57	Medium	97	-59
Globefish	0.005	-0.038**	-0.056*	S >>> I >>> D	67	-53	-74	High	106	38
Species with trend change point in 2000 in deep region										
Spiny gurnard	0.031	-0.036*	-0.025	S >>> I = D	127	-66	-43	Low	2	-9
Species without change point in deep										
Southern fiddler	0.018	0.008	-0.025	S = I >>> D	94	-13	-82	Low	20	1552
Sparsely spotted stingaree	0.001	-0.015	-0.036**	S >>> I >>> D	30	-4	-42	Low-medium	1	-23
Mixed feeders										
Species with step change point 1999 in deep region										
Yank flathead	0.019	0.024	0.035*	S = I = D (S < D)	102	78	100	Very low	47	-17
Species with trend change point in 2000 in deep region										
Sand flathead	-0.039*	-0.078***	-0.063***	S >>> I < D	-66	-91	-83	Low	-45	4

^aBased on mean biomass 1996–1997 cf. mean biomass 2009–2010; ^bZero biomass in 2010

mediate or deep) were extrapolated from swept area calculations, based on the capture efficiency of each species by the demersal trawl net (Parry 2011, Hirst et al. 2014) and the total area of each region. Similarly, regional estimates of the biomass of *Asterias amurensis* between 1998 and 2003 were obtained from swept area calculations of a modified scallop dredge used to survey starfish (Parry et al. 2004). Each bay-wide survey of *A. amurensis* involved 58 to 166 tows of a 2.7 m wide modified scallop dredge covered with 25 mm mesh to collect juvenile starfish, which was towed behind a vessel for 1 min. The diameter of each *A. amurensis* collected was measured to the nearest 5 mm. Biomass estimates were obtained from density estimates, the size–frequency distribution of starfish in each tow, and the relationship between *A. amurensis* diameter and mass (Parry et al. 2004). Qualitative trends in *A. amurensis* biomass in each region between 1990 and 2011 were also obtained from trawl catches.

RESULTS

Demersal fish biomass trends in Port Phillip Bay: 1990 to 2011

During the drought (1997 to 2010), total fish biomass declined by 69% in the deep region and 50% in the intermediate region, but there was no significant change (+35%) in the shallow region (Table 2, Fig. 2). The decline in total biomass in the deep region was largely explained by significant declines in the biomass of OBF (-65%), including eagle ray (-78%), eastern shovelnose stingaree (-57%), globefish (-74%) and sparsely spotted stingaree (-42%), and a significant decline in the biomass of mixed feeders (-73%), mostly due to a decline in sand flathead (-83%) (Table 2). The decline in the intermediate region was mostly due to a decline in the bio-

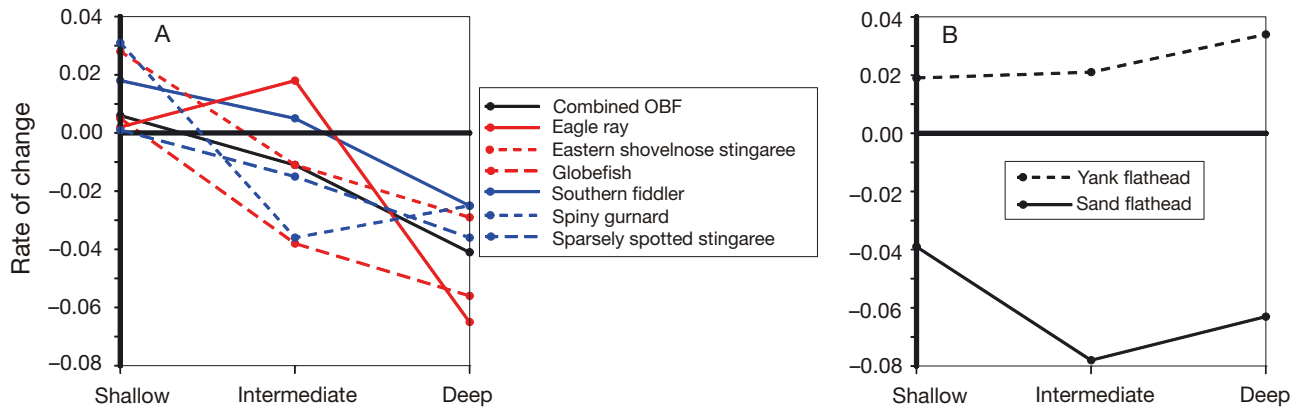


Fig. 2. Rates of change of fish biomass during drought (from Table 2) in each region (shallow, intermediate and deep) of Port Phillip Bay; (A) obligate benthic feeders (OBF), (B) mixed feeders

mass of mixed feeders (-87%), itself primarily due to a decline in sand flathead (-91%) (Table 2). Only 2 species increased significantly in biomass during the drought: eastern shovelnose stingaree in the shallow region ($+54\%$) and yank flathead in the deep region ($+100\%$) (Table 2).

Analysis of covariance showed that the rate of decline in biomass tow^{-1} during the drought was typically smallest for the shallow region and greatest for the deep region (Table 2, Fig. 2). The rate of decline was significantly lower for the shallow region than for the intermediate region for 7 of the 11 groupings/species considered (total biomass, mixed feeders, OBF, globefish, sand flathead, sparsely spotted stingaree and spiny gurnard; Table 2, Fig. 2). The rate of decline was significantly lower in the intermediate region than the deep region for all except 2 (spiny gurnard and yank flathead) of the 11 groupings/species considered (Table 2, Fig. 2).

The bcp analysis detected 20 change points with a posterior probability exceeding 0.50 (Figs. 3–5). All change point analyses showed convergence, using both tests employed. Posterior probabilities were not sensitive to missing data in 1998 and 2001. However, all significant change points ($p > 0.5$) in 2000 became significant change points in 2001 when average values were used to estimate the missing catches for 1998 and 2001. Hence, all these change points have been assigned to 2000/2001, reflecting the uncertainty of when the change occurred. Seventeen of the change points occurred in the deep region, 3 in the intermediate region and none in the shallow region (Figs. 3–5). All except 4 change points involved reductions in biomass, the exceptions being increases in the deep region for OBF biomass in 1991, for yank flat-

head in 1999 (Fig. 5) and for total fish biomass and mixed feeder biomass in 2010 (Fig. 3).

In contrast, STARS identified 43 change points with $p > 0.05$ (Figs. 3–5), indicating it detected more, smaller change points. Change points identified by STARS were also more equally distributed between regions, with 13 in the intermediate region and 15 in both the shallow and deep regions. In general, there was concordance between change points identified by both methods, although typically the STARS method identified a change the year after that identified by bcp. The exceptions occurred where there was a strong trend in the time-series (e.g. in the deep region: total fish, mixed feeding group and sand flathead, Figs. 3 & 5), where both methods appear to incorrectly interpret a strong trend as a series of change points (see 'Materials and methods'). The other discrepancy between methods occurred with yank flathead, where bcp identified 3 change points between 1994 and 1999 in the deep region, while STARS identified none (Fig. 5). In general, bcp is well-suited to detecting short-term fluctuations (Erdman & Emerson 2007), whereas STARS would not be able to detect changes shorter than the 8 yr cut-off length used in this study (Rodionov 2004).

Four significant bcps occurred for total fish biomass: 1 in the intermediate region in 2005 and 3 in the deep during 2000/2001, 2007 and 2010 (Fig. 3). The change point in the intermediate region in 2005 was mainly due to a decline in mixed feeders, while the 3 change points in the deep were due to a decline in OBF in 2000, a decline in mixed feeders in 2007 and an increase in mixed feeders in 2010 (Fig. 3). Between 2010 and 2011, total fish biomass increased by 102%, mainly due to a sharp increase in mixed feeders ($+119\%$) (Fig. 3).

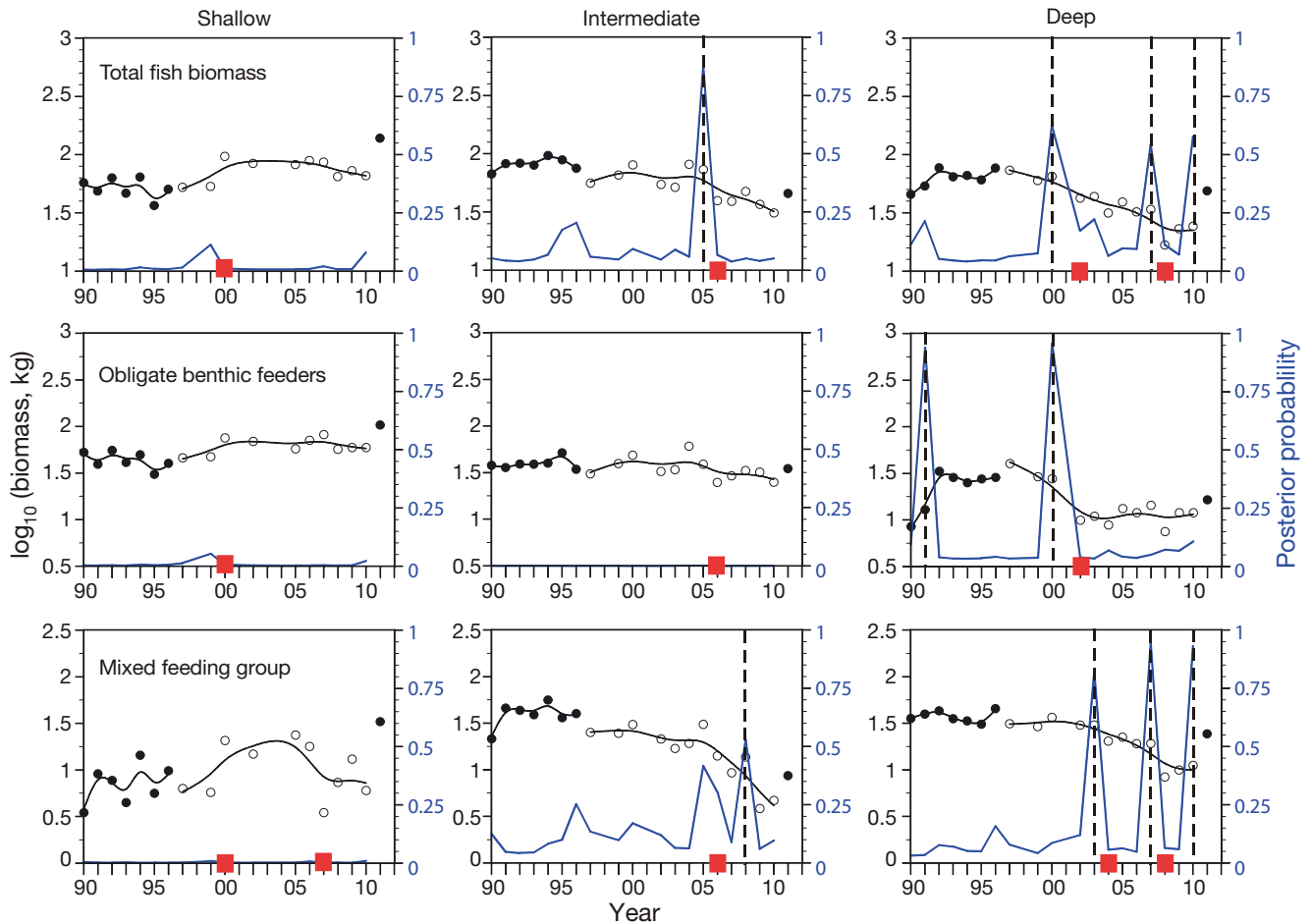


Fig. 3. Trends in \log_{10} biomass (kg) for total fish biomass and 2 trophic groups (obligate benthic feeders and mixed feeders) in the shallow, intermediate and deep regions of Port Phillip Bay from 1990 to 2011. Open circles were sampled during the drought. Bayesian change point (bcp) posterior probabilities are plotted in blue on the right hand scale, while change points obtained by 'STARS' are shown as red squares. Vertical lines indicate the position of bcps with posterior probability of change > 0.5 . Trend lines fitted using smoothing splines

Two significant bcps occurred for OBF; both in the deep region in 1991 and 2000/2001 (Fig. 3). The 1991 change point corresponded to increases in the biomass of many individual species, but no species had a significant change point in 1991 (Fig. 4). The 2000/2001 change point was the strongest temporal signal to emerge from the bcp analysis, and corresponded to significant change points for eastern shovelnose stingaree, globefish and spiny gurnard as well as a strong change point for eagle ray (Fig. 4).

Four significant bcps occurred for mixed feeders: 1 in the intermediate region in 2008, and 3 in the deep region in 2003, 2006 and 2010 (Fig. 3). The change point in the deep region in 2006 corresponded to a change point for sand flathead, but none of the other change points for mixed feeders corresponded to change points for either sand or yank flathead (Fig. 5). Other change points for sand flathead oc-

curred in the deep region in 2000/2001 and 2008 (Fig. 5). Three bcps occurred for yank flathead in the deep region between 1994 and 1999 (Fig. 5).

Environmental trends in Port Phillip Bay: 1985 to 2011

Coincident with the drought from 1997 to 2009, freshwater river flows into Port Phillip Bay declined substantially from 1997 onwards (Fig. 6A); salinity in the centre of the bay increased from 34 to 37 (Fig. 6B) and total nitrogen inputs declined by 64%, due to a 75% decline in nitrogen inputs from the catchment and a 56% decline in inputs from the WTP (Fig. 6C). All of the above changes were at least partially reversed in 2010 following drought-breaking rain (Fig. 6).

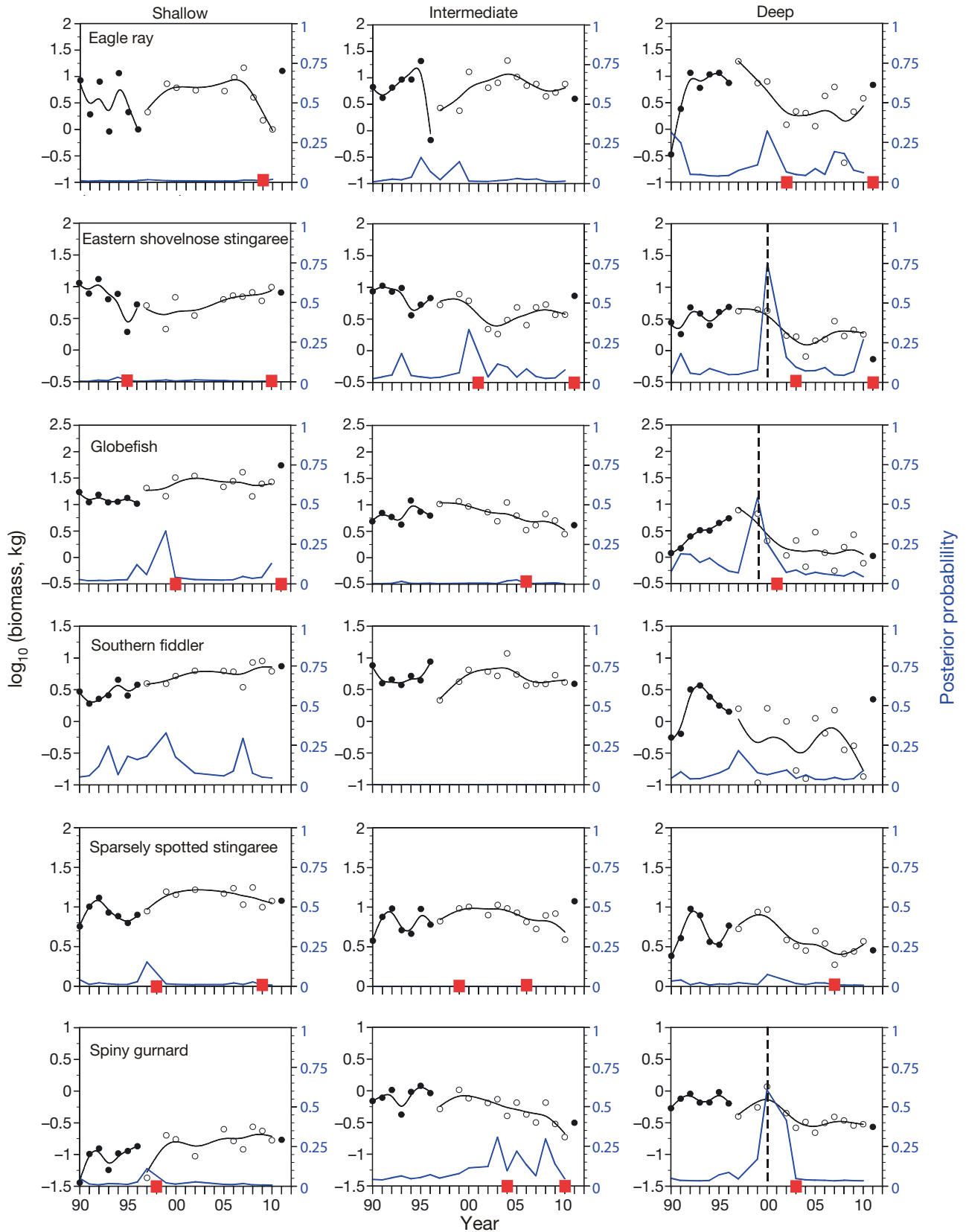


Fig. 4. Trends in \log_{10} biomass (kg) for 6 species of obligate benthic feeders in 3 regions (shallow, intermediate and deep) of Port Phillip Bay from 1990 to 2011. Open circles were sampled during the drought. Bayesian change point (bcp) posterior probabilities are plotted in blue on the right hand scale, while change points obtained by 'STARS' are shown as red squares. Vertical lines indicate the position of bcps with posterior probability of change > 0.5. Trend lines fitted using smoothing splines

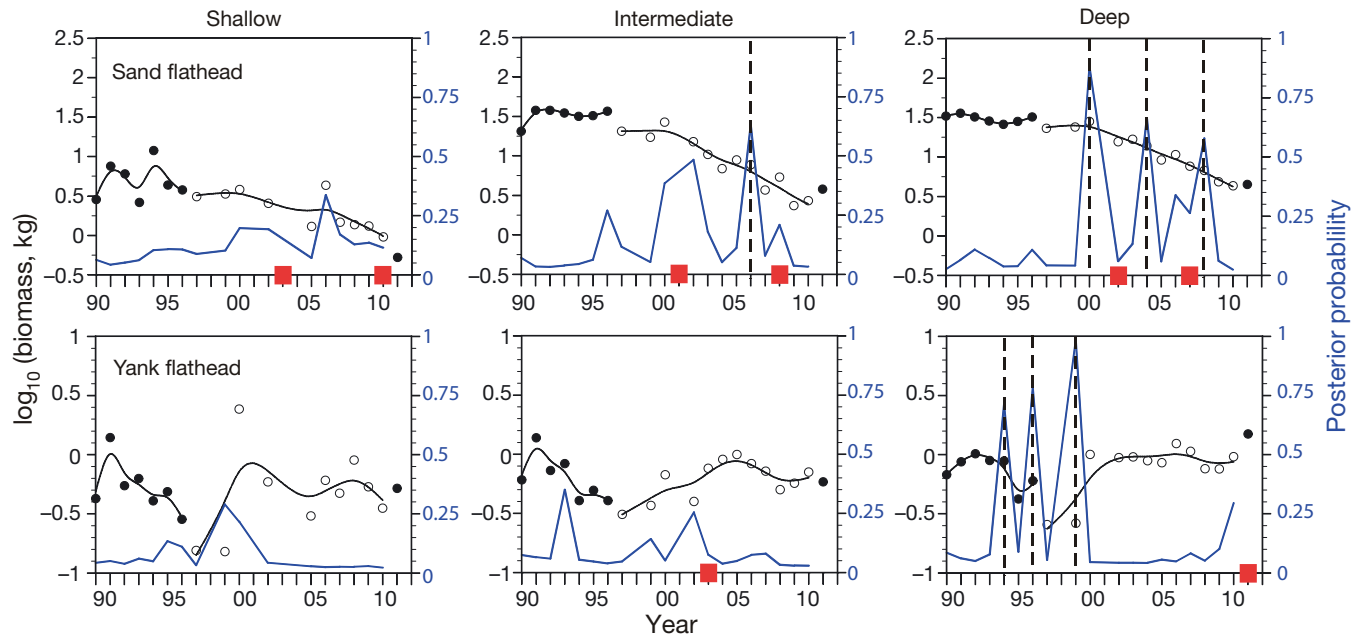


Fig. 5. Trends in \log_{10} biomass (kg) for 2 species of mixed feeders in 3 regions (shallow, intermediate and deep) of Port Phillip Bay from 1990 to 2011. Open circles were sampled during the drought. Bayesian change point (bcp) posterior probabilities are plotted in blue on the right hand scale, while change points obtained by 'STARS' are shown as red squares. Vertical lines indicate the position of bcps with posterior probability of change > 0.5. Trend lines fitted using smoothing splines

Table 3. Percentage of different speeds of winds in the pre-drought period (1992 to 1996) and during the drought (1997 to 2009) at Pt. Wilson. No wind measurements were made before 1992

Wind direction	Winds < 25 km h ⁻¹		Winds > 25 km h ⁻¹		Winds > 40 km h ⁻¹	
	1992–1996	1997–2009	1992–1996	1997–2009	1992–1996	1997–2009
All directions	62.10	61.94	37.90	38.06	7.31	6.96
West component	50.23	47.90	12.37	12.16	1.69	1.78
East component	34.67	36.88	2.72	3.06	0.36	0.30
North component	41.51	40.38	10.04	9.02	2.36	1.94
South component	39.83	41.00	8.63	9.60	5.27	7.04

Wind is usually the main influence on coastal circulation (Mann 1993), and in Port Phillip Bay it is the main driver of the large central gyre (Black et al. 1993). Drought-related changes in wind speed and direction were analysed to determine if they were likely to affect circulation patterns in the bay during the drought. Analysis of wind data from Pt. Wilson indicated there were only small differences in wind speed and direction between pre-drought (1992 to 1996) and drought years (1997 to 2009) (Table 3). Between the pre-drought and drought periods, frequencies of different wind speeds (<25, >25 or >40 km h⁻¹) varied by less than 0.5% (Table 3). Low speed (<25 km h⁻¹) westerly winds were 2.3% less frequent and easterly winds 2.2% more frequent during the drought. Changes in frequencies of winds of

different speeds and directions between pre-drought and drought periods were always much smaller than inter-annual differences (see Figs. S1–S3 in the Supplement at www.int-res.com/articles/suppl/m544_p037_supp.pdf).

Asterias amurensis was introduced into Port Phillip Bay in 1995, and by 2000 its population biomass had peaked at 2800 t (Parry et al. 2004), most of which was in the deep central region of the bay (Fig. 7). During March 2000, *A. amurensis* biomass was equivalent to 56% of total fish biomass in the deep region, 10% of total fish biomass in the intermediate region and 5% of total fish biomass in the shallow region (Fig. 7). After 2000, its biomass declined and was estimated at 1200 t in 2003. *A. amurensis* abundance in Port Phillip Bay was not quantitatively mon-

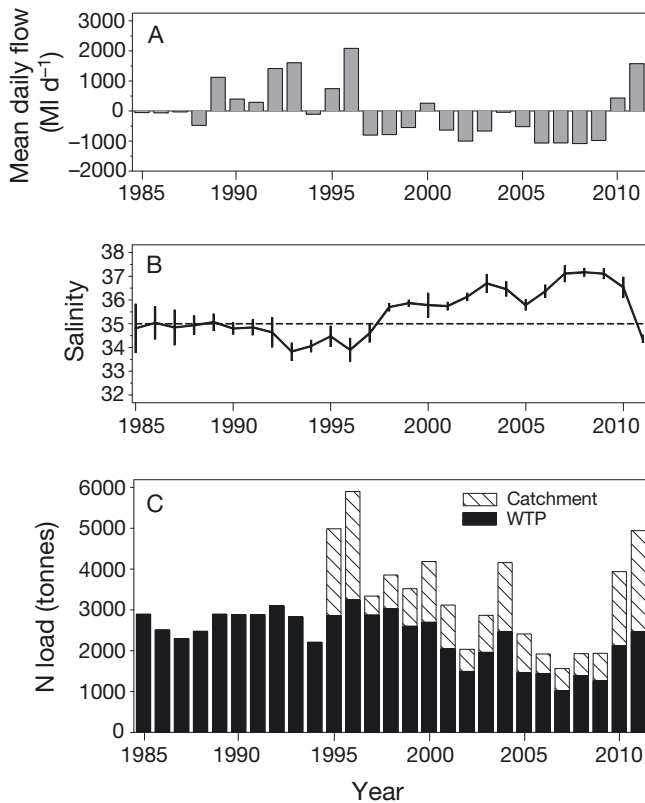


Fig. 6. Environmental trends in Port Phillip Bay, showing (A) annual anomalies in mean daily flows for the Yarra River from 1985 to 2011, (B) salinity (\pm SE) near the centre of the bay and (C) annual nitrogen load discharged from the Western Treatment Plant (WTP) and the bay's catchment. Estimates of catchment loads were not available before 1995

itored after 2003, although qualitative estimates from the annual trawl survey (Fig. 7D) indicate that its biomass has remained highest in the deep and lowest in the shallow region.

DISCUSSION

Large declines in the biomass of demersal fish in Port Phillip Bay between 1990 and 2011 coincided with 2 major ecological disturbances: a drought (1997 to mid-2010) which reduced nitrogen inputs into the bay by 64%, and the introduction of an exotic starfish, whose biomass in the deep centre of the bay peaked at 56% of the resident fish biomass in 2000.

Hydrodynamic modelling suggested that during drought conditions, a greater proportion of the overall production would remain near the coast (Lee et al. 2012). During the drought, the lower momentum of the smaller discharges reduced the initial penetration of the inputs so that shortly after discharge,

nutrient-enriched water remained nearer the coast. Most nutrients are delivered to the north (Yarra River) and northwest (WTP) areas of the bay (Fig. 1), where they are quickly taken up by phytoplankton and subsequently, zooplankton. These are typically entrained in a large clockwise gyre that occupies much of the bay (Black et al. 1993, Lee et al. 2012). Modelling by Lee et al. (2012) showed that in response to increased salinity in the bay during the drought (where it increased from 34 to 37), the current strength in the gyre increased. Both the reduced input momentum and the stronger gyre during the drought increase the average path length for passive particles between coastal inputs and the centre of the bay, ensuring that these particles spend longer in the shallow region. Consequently, a higher proportion of the nutrients, along with the phytoplankton and zooplankton derived from them, will be stripped from the water column before they reach the deep central region.

Drought-related changes in circulation caused by changes in wind speed and direction were minimal. There were only small differences in wind speed and direction between pre-drought (1992 to 1996) and drought years (1997 to 2009), and these differences were much smaller than inter-annual differences. Thus, changes in circulation caused by wind are likely to have affected inter-annual differences in circulation patterns, but are unlikely to have caused systematic differences between the drought and pre-drought periods.

Declines in fish biomass due to drought-related changes in productivity were expected to cause gradual declines in fish biomass between 1997 and 2010, and to be greatest in the deep centre of the bay and least around the shallow edges. Competition with starfish was also expected to have its greatest impact in the deep region (where they were most abundant), but starfish were expected to cause a sharp decline in 2000, when their biomass peaked. A sharp decline was expected as the *Asterias* biomass increased rapidly from near zero in 1998 to 2800 t in 2000, and the growth rate of individual *Asterias* declined sharply between 1999 and 2000. A 1 yr old *Asterias* in 2000 weighed only one-fifth the weight of an *Asterias* of this age in 1999 (Parry & Cohen 2001), suggesting a rapid increase in competition for food in 2000. Competition with *A. amurensis* was also most likely to occur with species whose diets overlapped most with those of *A. amurensis*.

The gradual baywide decline in total fish biomass during the drought, and the large increase in biomass in 2011 following drought-breaking rain, were

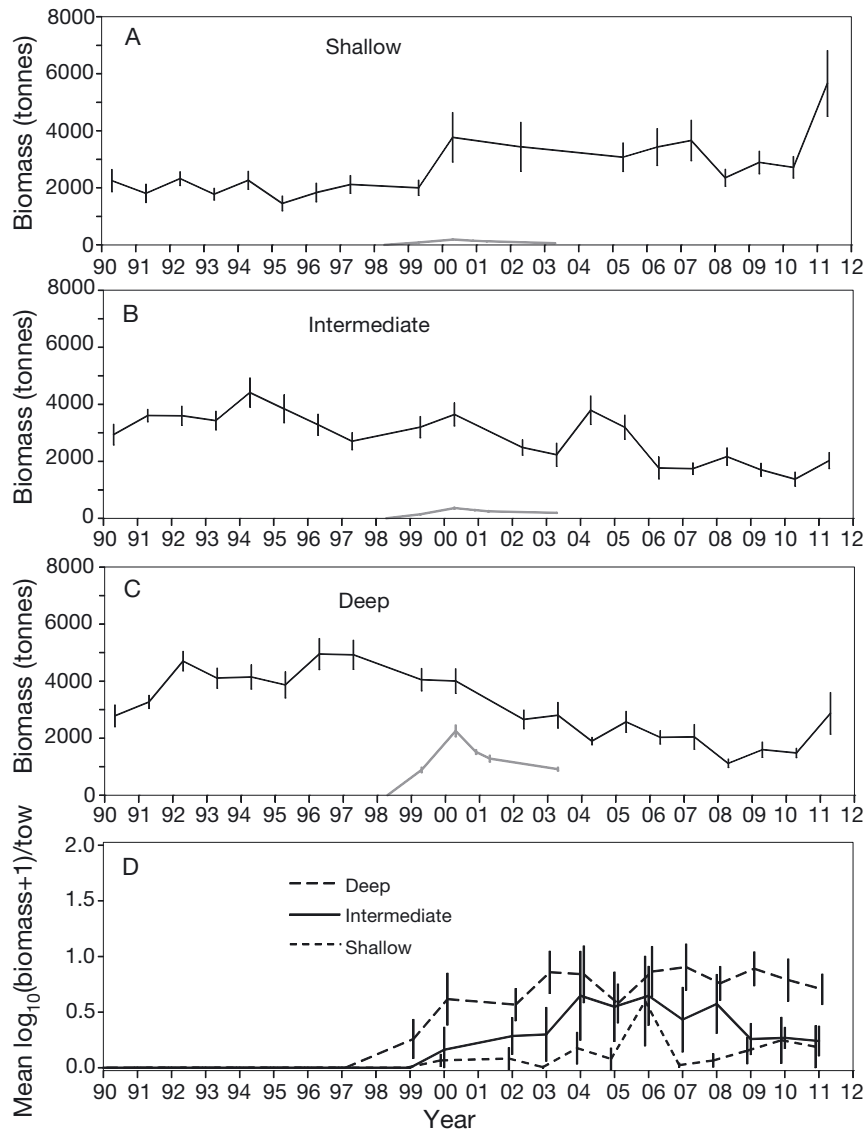


Fig. 7. Mean (\pm SE) total fish (black line) and *Asterias amurensis* (grey line) biomass (tonnes) in (A) shallow, (B) intermediate and (C) deep regions of Port Phillip Bay, based on swept area measurements for trawl net and a modified scallop dredge for *A. amurensis*. (D) Index of abundance for *A. amurensis* based on trawl catches, for 3 regions of Port Phillip Bay between 1990 and 2011

consistent with expectations that reduced nutrient inputs would lead to reduced productivity and lower fish biomass (Loneragan & Bunn 1999). That the decline in fish biomass during the drought was greatest in the deep region and least in the shallow region was also consistent with predicted regional changes in nutrient delivery due to changes in circulation patterns.

Declines in southern fiddler ray and sparsely spotted stingaree in the deep region were also considered to have been mostly due to the drought. Both these species declined gradually during the drought

without significant change points (Fig. 4). This interpretation is also consistent with the minimal overlap between their diets and that of *A. amurensis*. Southern fiddler ray feed on fish (including sand flathead) and large crustaceans, while sparsely spotted stingaree mostly feed on small and medium-sized crustaceans (Parry et al. 1995).

The abrupt declines in biomass of fish between 2000 and 2002, coincident with the peak in *Asterias* biomass, were of particular interest. Unfortunately, no change point method is likely to unambiguously identify a step change in fish biomass at this time, as many species were trending down during the sustained drought (1997 to 2010). All methods of change point analysis are compromised when there is a temporal trend, which may be incorrectly identified as a step change (or changes) in the middle of the trend (See 'Materials and methods').

Step-like declines in OBF biomass in the deep region in 2000/2001, coincident with step-wise declines in eastern shovelnose stingaree, eagle ray (change point $p = 0.32$; Fig. 4) and globefish suggest that these declines were probably due to competition with *A. amurensis*. Further support for this interpretation comes from the substantial dietary overlap between these species and *A. amurensis*. Eagle ray and globefish feed mainly on molluscs (Parry et al. 1995), which is the preferred prey of *A. amurensis* (Grannum et al. 1996, Ross et al. 2004). Eastern shovelnose

stingaree feed primarily on polychaetes (Parry et al. 1995), which are also eaten by *A. amurensis* (Grannum et al. 1996, Lockhart & Ritz 2001), particularly when bivalves become rare (Ross et al. 2004).

The cause of the decline in spiny gurnard in the deep region is more ambiguous, although drought appears to be the primary cause. The change point for spiny gurnard recorded in 2000/2001 was not coincident with the STARS change point and is probably an artefact of the long-term decline that occurred at similar rates in both the deep and intermediate regions

(Fig. 4). The minimal overlap between the diets of spiny gurnard and *A. amurensis* suggests little competition between these species. Spiny gurnard feed mostly on amphipods (Parry et al. 1995), which have not been recorded in the diet of *A. amurensis* (Grannum et al. 1996, Lockhart & Ritz 2001).

The most spectacular decline during the drought occurred in sand flathead, and the drought appears to be the primary cause of this decline. This species had the highest biomass of any species in the bay during 1990 to 2000, but by 2010 its biomass had declined by up to 90% across all regions of the bay, and it was ranked only the 8th most abundant species. Hirst et al. (2014) analysed the age structure of the population between 1990 and 2011 and found that its decline resulted from a prolonged period of weak recruitment coinciding with the drought, which was directly linked to reduced river flows into the bay during this period. These conditions were thought to reduce the survival of larvae and subsequent recruitment of juvenile sand flathead (Hirst et al. 2014). Trends in the growth of this species determined from otolith increments (Rees 2013) suggest that competition with *A. amurensis* was unlikely to be important, as growth was above trend during 1999 and 2000 when *A. amurensis* biomass peaked in the bay. Sand flathead are mixed feeders with a diet that comprises both benthic and pelagic prey, and there is little overlap with the diet of *A. amurensis*. Changes in the availability of anchovies may explain inter-annual trends in growth as the % volume of anchovies in sand flathead guts collected during trawl surveys varied from 0% (1993, n = 172 and 1997, n = 91) to 71% (2004, n = 178) in the deep region (G. D. Parry unpubl. data).

In contrast to all other species, the biomass of yank flathead increased in all regions. Yank flathead feed mostly on clupeoids (Parry et al. 1995), and the abundance of their prey changed markedly during 1990s. Pilchards, the most abundant zooplanktivore in the bay, were greatly reduced in 1995, and almost disappeared in 1998 following collapse of the stock across all of southern Australia, apparently due to 2 outbreaks of an exotic virus (Gaughan et al. 2000). In South Australia, the loss of pilchards was correlated with a large increase in the abundance of anchovies (Ward et al. 2001). The 3 strong bcps between 1994 and 1999, coincident with the near disappearance of pilchards in the bay and a possible increase in anchovies, suggest that changes in yank flathead were probably due to changes in the abundance of clupeoid prey, and largely unrelated to either the drought or *A. amurensis*.

Fishing pressure is unlikely to have significantly influenced changes in biomass of most fish. Only 2 of the 8 species considered individually (sand flathead and yank flathead) were targeted by fishers, and catches of non-targeted species were minimal. Of the 6 non-targeted species, spiny gurnards and stingarees are never caught on lines, while globefish, southern fiddlers and eagle rays are rarely caught.

Of the 8 species considered individually, sand flathead was the only species for which there is evidence from missing age classes in the age structure of the population that recruitment was low throughout the drought. The decline in sand flathead biomass during the drought was the result of minimal recruitment and ongoing mortality. While Hirst et al. (2014) estimated that recreational fishing removed at least 15% of the sand flathead biomass annually in 2000 and 2006, the relative contributions of fishing and natural mortality remain unmeasured. That recruitment failure initiated the decline is consistent with sand flathead being the only species that declined across all regions. As yank flathead increased in abundance in all regions during the drought, it is possible that its increase was also due to increased recruitment, but no information on its age structure during the study period is available. The remaining species included 4 chondrichthyans that have no planktonic larval phase, and globefish and spiny gurnard, whose abundance declined in the intermediate and deep regions but not in the shallow region. The biomass of these species probably declined as a result of increased mortality rates due to food shortage, although the larger species (eagle ray and southern fiddler ray) are known to migrate seasonally (Parry et al. 1995), and may have moved out of the bay.

The rebound in total fish biomass between 2010 and 2011, mainly due to an increase in mixed feeders and pelagic species, is probably due to increased planktonic productivity that accompanied high rainfall at the end of the drought in mid-2010. The first winter storm after a drought typically contains an unusually high nitrate concentration (Sigleo & Frick 2007, Lake 2011), and increased nutrient inputs are likely to have contributed to a rapid increase in planktonic productivity. In 2011, pelagic species in the deep region made up 17% of the total biomass, more than 4 times their contribution during the drought. Similarly, the pelagic piscivores yellowtail scad *Trachurus novaezelandiae* and barracouta *Thyrsites atun* were ranked 9th and 10th in 2011 catches, but were uncommon throughout the drought. That OBF showed a smaller increase than mixed feeders

between 2010 and 2011 suggests that planktonic productivity rebounded more quickly than benthic productivity.

There may also have been important interactions between the effects of the drought and competition with *A. amurensis*. *A. amurensis* has a large negative impact on the densities of native bivalves (Ross et al. 2002, 2004), which comprise a large proportion of the benthic fauna in Port Phillip Bay (Wilson et al. 1998). The loss of these filter and suspension feeders may have reduced the coupling between benthic and pelagic productivity and reduced nutrient cycling (Wilson et al. 1993). These changes may have exaggerated the impact of the drought in areas heavily infested with *A. amurensis*. Conversely, declines in the biomass of eagle ray, globefish and eastern shovelnose stingaree, attributed to competition with starfish, were similar to the long-term rates of decline of drought-affected species so it is possible that *A. amurensis* caused a sharp decline in these species in 2000, but their low biomasses persisted until 2010 due in part to the drought.

CONCLUSIONS

This study provides strong evidence that fish biomass in a temperate embayment declined as nutrient inputs declined during a prolonged drought. The decline in 4 species (southern fiddler ray, sparsely spotted stingaree, spiny gurnard and sand flathead) were most likely caused by reduced nutrient inputs. It is likely that significant correlations were detected in this study because reductions in nutrient inputs were sustained across many years. Productivity-related changes in fish abundance are probably widespread in temperate regions, but difficult to detect due to the variation inherent in sampling fish and the usually short duration of reduced nutrient inputs.

This study is also the first to suggest that *Asterias amurensis* has caused large changes to marine fish populations. Despite its status as a highly noxious marine pest (Hayes et al. 2005), the ecological impacts of *A. amurensis* have previously been inferred from small scale experiments. In Port Phillip Bay, the impacts occurred principally amongst fish species that feed on molluscs and polychaetes in areas where *A. amurensis* densities were highest.

The link between nutrient inputs and fish abundance has implications for management of inputs from catchments and treated sewage plants in coastal locations world-wide, but particularly in semi-enclosed water bodies such as Port Phillip Bay.

Reductions in nutrient inputs minimise the likelihood of undesirable changes (algal blooms, establishment of exotic algae adapted to eutrophic conditions), but may also reduce fish production. Southeastern Australia's future climate is also expected to become drier as a consequence of anthropogenic global warming (Christensen et al. 2013), and droughts are expected to be more common (Power et al. 2013, Santoso et al. 2013). The implications of changing catchment and treated sewage inputs of nitrogen into the bay need to be better understood; thus, we hope that our findings encourage the development of more sophisticated production models that may assist in more fully understanding the impact of past and future changes in nutrient inputs to Port Phillip Bay.

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