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Effects of flood and drought events on multi-species, multi-method estuarine and coastal fisheries in eastern Australia

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Abstract Multivariate patterns in commercial fisheries landings, effort and revenue from three adjacent estuarine and coastal systems were examined in eastern Australia between 9-month periods of flood (September 2000–May 2001) and drought (September 2002–May 2003). Patterns in species landings, methods of fishing effort and revenue per species were significantly different between flood and drought. Spearman's rank correlations between Bray–Curtis similarity matrices for landings, effort and revenue indicated that patterns in fisheries metrics represented a mixed signal of ecological response and fishers' harvesting behaviour. Flood and drought events were associated with shifts in the species composition of landings that were reciprocated between estuarine and coastal systems. Estuarine migrant species (e.g. school prawn *Metapenaeus macleayi* Haswell) primarily contributed to landings during drought. Flood and drought events redistributed fisheries resources between estuarine and coastal systems, modifying the bioeconomic productivity of commercial fisheries. Results indicated that flood and drought events influence commercial fisheries by modifying landings composition, fishers' harvesting behaviour.

KEYWORDS: bioeconomic productivity, commercial fisheries, harvesting behaviour, landings composition, revenue generation.

Introduction

Understanding linkages between freshwater flow and coastal fish communities is an important issue in fisheries ecology (Gillanders & Kingsford 2002). Freshwater flow is a critical landscape process that regulates the physical, chemical and biological properties of coastal marine ecosystems (Skreslet 1986). Natural variability in freshwater flow strongly influences the distribution and abundance of fish communities by altering habitat availability and trophic dynamics in estuarine and coastal systems (Kimmerer 2002; Darnaude *et al.* 2004; Lamberth *et al.* 2009). Seasonal and interannual shifts in the composition of fish communities can occur due to natural fluxes in the

flow regime modifying the distribution and abundance of marine, estuarine and freshwater species (Hurst *et al.* 2004; Costa *et al.* 2007; Baptista *et al.* 2010). Alterations to freshwater flow have a marked influence on coastal fish communities and any dependent fisheries (Drinkwater & Frank 1994).

Freshwater flow has a pivotal role in determining fisheries production due to its effects on environmental conditions in estuarine and coastal systems (Loneragan & Bunn 1999; Grimes 2001; Lloret *et al.* 2004). Freshwater enhancement of fisheries production operates via several interrelated mechanisms: (1) increased growth and survival due to nutrient enrichment increasing primary and secondary production (Darnaude *et al.* 2004); (2) alterations to abundance resulting from

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salinity fluctuations modifying habitat availability (Kimmerer 2002); (3) changes to migration and schooling altering catchability (Loneragan & Bunn 1999); and (4) improved recruitment due to increased offshore concentrations of land-based cues stimulating fish larvae to immigrate into estuarine nursery grounds (Vinagre *et al.* 2007). Despite well-established linkages between freshwater flow and fisheries production (Caddy & Bakun 1995), the effects of flood and drought events on multi-species and multi-method fisheries in estuarine and coastal systems have received little attention.

Flood and drought events are pulse disturbances that maintain biological productivity in estuaries (Flint 1985; Martin et al. 1992; Dolbeth et al. 2008). Episodic flow events are important determinants of estuarine fisheries production in eastern Australia (Gillson et al. 2009). Nevertheless, the effects of flood and drought events on the availability of fisheries resources and the dynamics of commercial fisheries in eastern Australia remain unclear. Eastern Australia experiences extreme hydrological conditions (Finlayson & McMahon 1988), with climatic variability driving sporadic rainfall and stochastic flow events (Power et al. 1999). Coastal rivers in this region are influenced by alternating flooddominated and drought-dominated regimes (Erskine & Warner 1998), with fresh water primarily delivered into estuaries by episodic flow events (Eyre 1998).

Environmental fluctuations influence fish population dynamics by modifying ecological processes, which in turn produces cascading effects on fishing activity and the economic productivity of commercial fisheries that operate in estuarine and coastal systems (Pauly et al. 2002; Link & Tol 2006; Rouver et al. 2008). An improved understanding of interactions between environmental variation, the availability of fisheries resources and the operational characteristics of commercial fisheries is essential for the development of an ecosystem-based approach to fisheries management (Hall & Mainprize 2004). Flood and drought events should impact the species composition of commercial landings, fishers' harvesting behaviour and the economic performance of estuarine and coastal fisheries in eastern Australia. This prediction was tested using the following hypotheses. Firstly, changes in the species composition of landings between flood and drought will result from differences in the life history characteristics and habitat preference of individual species. Secondly, fishers' will modify their harvesting behaviour between flood and drought primarily to exploit alterations in species landings. Thirdly, revenue generation will fluctuate between flood and drought primarily because of variation in landings rather than the market price per species.

This study conducted a multivariate analysis of commercial fisheries metrics from three adjacent estuarine and coastal systems in eastern Australia between periods of flood and drought. This research represented a multivariate extension of a previous study that focused on the impacts of drought on the catch rates of a single-method gillnet fishery (Gillson *et al.* 2009). The objectives of this study were to: (1) examine multivariate patterns in the species composition of landings and revenue between flood and drought; and (2) investigate multivariate patterns in landings, effort and revenue between flood and drought.

Methods

Study areas

Three adjacent estuarine and coastal systems along the eastern Australian coastline were selected to evaluate the impacts of flood and drought events on multispecies, multi-method fisheries (Fig. 1). Estuarine fisheries were located in the permanently open lower reaches of the Clarence, Hunter and Hawkesbury River systems. Adjacent coastal fisheries extended approximately 30 km onto the continental shelf and approximately 0.5° north and south of each river system (i.e. coastal zones 2, 5 and 6). The spatial extent of coastal fisheries was based on reporting zones used by the Industry and Investment New South Wales (I&I NSW). These estuarine and coastal fisheries employ a variety of fishing methods to target commercially important species of penaeid prawns, finfish, sharks and crabs (Pease 1999; Saintilan 2004; Ives et al. 2009). We selected these fisheries for investigation because they provide the dominant contribution to commercial harvest in NSW (Table 1), and the neighbouring river systems exhibit highly variable annual flows with a coefficient of variation (C_v) of more than 75% (Finlayson & McMahon 1988). Annual variation in freshwater flow from eastern Australian rivers exceeds the world average by a factor of more than 1.8 (Peel et al. 2001). The El Niño-Southern Oscillation (ENSO) generates sporadic rainfall and unpredictable flow events in this region (Power et al. 1999). Coastal rivers in eastern Australia can experience prolonged periods of drought that are punctuated by sporadic flood events (Erskine & Warner 1998).

Hydrological data

Nine-month periods of flood (September 2000–May 2001) and drought (September 2002–May 2003) were identified in the Clarence, Hunter and Hawkesbury



Figure 1. Location of three adjacent estuarine and coastal systems selected to investigate the impacts of flood and drought events on multi-species and multi-method fisheries in eastern Australia (a). Freshwater flow [•] gauging stations shown in relation to the estuarine and coastal reaches of the Clarence (b), Hunter (c) and Hawkesbury (d) River systems.

River catchments. These periods of flood and drought were defined by the Australian Bureau of Meteorology 2010 (http://www.bom.gov.au/climate). Monthly freshwater flow data from September 2000 to May 2001 and September 2002 to May 2003 were extracted from the Pinneena 9.1 database of the New South Wales Department of Water and Energy (NSW DWE) for the Clarence and Hunter Rivers and obtained from the Sydney Catchment Authority (SCA) for the Hawkesbury River. Gauged freshwater flow data were provided for the Clarence River at Lilydale; the Hunter River at Greta; and the Hawkesbury River at Yarramundi, Burralow, Richmond, Cattai Ridge, Upper Colo, St. Albans and Riverstone. Freshwater flow data included spring to autumn periods in temporally adjacent flood and drought phases.

Fisheries data

Monthly commercial fisheries landings, effort and Sydney Fish Market price data were compiled from the I&I NSW ComCatch database from September

ries (Pease 1999). Mean flow (ML d ⁻¹ month ⁻¹) represents mean monthly freshwater flow in ML d ⁻¹ between 1997 and 2007 (note that 1 ML d ⁻¹ tiver regulation describes the amount of freshwater regulation and extraction within a catchment. Mean landings (t month ⁻¹), percent of fisheries d mean revenue (AU\$000 month ⁻¹) indicate mean landings in t month ⁻¹ , the percentage contribution to monthly commercial fisheries harvest in the mean revenue in AU\$000s per month, respectively, between 1997 and 2007	$ \begin{array}{ccccc} Fisheries & Catchment & Mean flow & River & Mean landings & Percent of & Mean effort & Mean revenue \\ ude & bioregion & area (km^2) & (ML \ d^{-1} \ month^{-1}) & regulation & (t \ month^{-1}) & fisheries \ harvest & (days \ month^{-1}) & (AU \ S000 \ month^{-1}) \\ \end{array}$	19.20'E Northern 22 400 181 946 Moderate 149 16 1160 522.9 33.59'E Central 22 000 53 608 High 79 9 444 167.9 23.40'E Control 21 600 65 353 High 62 7 478 113.0
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Fisheries metrics included landings (kg per month), effort (days fished per month) and revenue (AU\$ per month) for 27 species groups and 16 fishing methods that contributed >95% of harvest between July 1997 and June 2007 (Tables 2 and 3). Life history information (e.g. reproductive characteristics, migration patterns and physiological adaptations) and habitat use (e.g. riverine, estuarine and marine) were considered before assigning individual species into one of seven estuarine use guilds: (1) amphidromous (AM; species that migrate between freshwater and marine habitats but not for reproductive purposes); (2) catadromous (CA; species that primarily inhabit freshwater habitats but migrate out to sea to spawn); (3) estuarine migrant (EM; species that have larval stages of their life cycle completed outside an estuary); (4) estuarine resident (ER; species capable of completing their entire life cycle within an estuary); (5) marine estuarine dependent (MD; species that depend on sheltered estuarine habitats as juveniles); (6) marine estuarine-opportunist (MO: species that opportunistically enter estuaries in substantial numbers but use nearshore marine waters as alternative habitat); and (7) marine straggler (MS; species that spawn at sea and typically enter the lower reaches of estuaries in low numbers when salinities are approximately 35. These species are often stenohaline and primarily inhabit coastal marine waters). A detailed description of the approach used to categorise species into estuarine use guilds has been presented in Elliot et al. (2007). Fisheries metrics were summed into monthly totals for individual species, guilds and fishing methods during periods of flood and drought. Difference indexes of landings per guild and revenue per guild were calculated by subtracting mean landings and revenue from each guild between periods of flood and drought.

Revenue per guild was calculated as:

$$R_{\mathrm{g},t} = \sum_{\mathrm{s}=1}^{n_{\mathrm{g}}} C_{\mathrm{s},t} \cdot \bar{P}_{\mathrm{s},t}$$

Where $R_{g,t}$ is revenue for guild g in month t (Australian dollars), $n_{\rm g}$ is the number of species in guild g, $C_{s,t}$ is the landings of species s in month t (kilograms) and $P_{s,t}$ is the mean market price per kilogram of species s in month t from Sydney Fish Market.

Data analysis

Freshwater flow data were \log_{10} transformed to normalise variances. Transformed freshwater flow data

2000 to May 2001 and September 2002 to May 2003.

Table 2. Summary of selected species groups used to examine the impacts of flood and drought events on estuarine and coastal fisheries
Estuarine use guilds consisted of amphidromous (AM); catadromous (CA); estuarine migrant (EM); estuarine resident (ER); marine estuarin
dependent (MD); marine estuarine-opportunist (MO); and marine straggler (MS). Landings and revenue refer to mean landings per month (
and mean revenue per month (AU\$000s), respectively, between 1997 and 2007

Estuarine use guild	Species group	Landings (t)	Revenue (AU\$000s)	
AM	Catfish (Siluriformes spp.)	1.5	2.8	
CA	River eels (Anguilla spp.)	3.9	12.6	
EM	Eastern king prawn (Melicertus plebejus)	36.2	716.5	
EM	School prawn (Metapenaeus macleayi)	43.1	299.2	
EM	Sea mullet (Mugil cephalus)	112.5	198.6	
EM	Giant mud crab (Scylla serrata)	2.1	34.8	
EM	Estuary squid (Uroteuthis spp.)	2.5	5.5	
EM	Silver scat (Selenotoca multifasciatus)	1.0	1.4	
ER	Trumpeter whiting (Sillago maculata)	1.5	5.9	
MD	Goldspot mullet (<i>Liza argentea</i>)	1.7	2.0	
MD	River garfish (Hyporhamphus regularis ardelio)	0.4	1.5	
MO	Yellowfin bream (Acanthopagrus australis)	10.4	89.5	
MO	Sand whiting (Sillago ciliata)	4.2	43.2	
MO	Silver trevally (Pseudocaranx georgianus)	13.0	34.1	
MO	Mulloway (Argyrosomus japonicus)	3.3	24.7	
MO	Sand mullet (Myxus elongatus)	17.8	21.8	
MO	Blue swimmer crab (Portunus pelagicus)	2.2	13.5	
MO	Dusky flathead (Platycephalus fuscus)	2.0	10.2	
MO	Tailor (Pomatomus saltatrix)	1.6	8.4	
MO	Largehead hairtail (Trichiurus lepturus)	0.9	8.0	
MO	Yellowtail scad (Trachurus novaezelandiae)	4.2	7.0	
MO	Luderick (Girella tricuspidata)	5.6	6.7	
MO	Sandy sprat (Hyperlophus vittatus)	1.7	5.6	
MO	Silver biddy (Gerres subfasciatus)	1.5	4.0	
MS	Blue spotted flathead (Platycephalus caeruleopunctatus)	7.8	25.6	
MS	Whaler sharks (Carcharhinus spp.)	4.8	14.9	
MS	Australian sardine (Sardinops neopilchardus)	3.5	11.9	

were normally distributed (Lillefors test) with no evidence of heteroscedasticity (standardised quantile plots). One-way analysis of variance (ANOVA) was used to compare freshwater flow between flood and drought.

Multivariate techniques were used to examine variation in landings, effort and revenue between flood and drought using the PERMANOVA + add-on package for PRIMER v6 (Clarke & Gorley 2006; Anderson *et al.* 2008). Separate analyses were undertaken for estuarine and coastal systems to determine whether multivariate patterns in landings, effort and revenue between flood and drought were consistent amongst the distinct fisheries. Bray–Curtis similarity matrices were constructed from fourth-root transformed data to reduce the weighting of frequently landed species and regularly used fishing methods whilst preserving information about relative contribution. Spearman's rank correlation coefficients (ρ) between Bray–Curtis similarity matrices for landings, effort and revenue were calculated using RELATE tests performed with 4999 permutations. Non-metric multidimensional scaling (MDS) ordination plots, based upon Bray-Curtis similarity matrices, were used to visualise multivariate patterns in landings, effort and revenue between flood and drought. A one-way permutational multivariate analysis of variance (PERMANOVA) was performed to test the statistical significance of visualised differences in landings, effort and revenue between flood and drought (Anderson et al. 2008). PERMANOVA models consisted of one fixed factor (flow condition) with two levels (flood and drought). P-values for PERMANOVA models were calculated using 4999 unrestricted permutations of raw data (Manly 1997). As a statistically significant result from PERMANOVA could indicate that the groups differ in their location and/or dispersion in multivariate space, a permutational analysis of multivariate dispersions (PERMDISP) was used as a post hoc test to compare heterogeneity in the multivariate dispersion of landings, effort and revenue between

Table 3. Summary of selected fishing methods used to examine the impacts of flood and drought events on estuarine and coastal fisheries. Gear type indicates whether fishing equipment is active or passive. Landings, effort and revenue refer to mean landings per month (t), mean effort per month (days) and mean revenue per month (AU\$000s), respectively, between 1997 and 2007

System	Fishing method	Gear type	Landings (t)	Effort (days)	Revenue (AU\$000s)
Estuarine	Estuarine prawn trawl	Active	37.1	854	255.7
	Gillnets	Passive	61.4	711	155.7
	Hauling net	Active	32.1	276	85
	Prawn set pocket net	Passive	4.7	69	34.6
	Crab pot	Passive	2.3	89	33.8
	Eel trap	Passive	3.8	127	12.3
	Bait net	Active	3.4	12	8.9
	Handline	Active	1.1	72	8.6
	Fish trap	Passive	0.8	51	6.1
	Bullringing	Active	0.5	10	1.9
Coastal	Ocean prawn trawl	Active	49.5	779	772.7
	Hauling net	Active	62.6	244	123.9
	Fish trawl	Active	14.8	196	44.6
	Fish trap	Passive	6.7	337	31
	Handline	Active	5.7	355	27.1
	Purse seine net	Active	5.7	17	15.7
	Bait net	Active	3.2	7	9.6

flood and drought. PERMDISP is a multivariate analogue of the Levene's test that assesses multivariate dispersion by comparing distances from observed vectors to their group centroid using 4999 permutations of residuals to calculate *P*-values (Anderson *et al.* 2008). A similarity percentage contribution analysis (SIMPER) was performed to identify species, guilds and methods that primarily contributed to average Bray– Curtis dissimilarities between flood and drought (Clarke & Gorley 2006).

Results

Freshwater flow

Freshwater flow was significantly different in the Clarence, Hunter and Hawkesbury Rivers between flood and drought events (Fig. 2). Flow magnitudes were considerably higher than the long-term (10-year) monthly means in Clarence (+472%), Hunter (+243%) and Hawkesbury (+165%) Rivers during flood. Drought conditions were characterised by flow magnitudes that were below the long-term (10-year) monthly means in the Clarence (-49%), Hunter (-84%) and Hawkesbury (-65%) Rivers.

Landings per guild

Non-metric multidimensional scaling ordination plots revealed detectable contrasts in estuarine and coastal landings per guild between flood and drought (Fig. 3), which were statistically significant (Tables 4 and 5). Heterogeneity in landings per guild between flood and drought arose from differences in the location of groups in multivariate space (PERMDISP, $P \ge 0.05$). Average dissimilarity in landings per guild between flood and drought was relatively high in the Clarence (16.9%), Hunter (12.7%) and Hawkesbury (10.3%) River estuaries. Estuarine migrant, estuarine resident and catadromous guilds primarily contributed to estuarine landings during flood. Marine estuarineopportunist, marine estuarine dependent and marine straggler guilds primarily contributed to estuarine landings during drought. Average dissimilarity in landings per guild between flood and drought was relatively low in the Clarence (7.9%), Hunter (6.2%)and Hawkesbury (4.6%) coastal systems. Marine estuarine-opportunist, marine straggler and marine estuarine dependent guilds primarily contributed to coastal landings during flood. Estuarine migrant and



Figure 2. Box and whisker plots illustrating significant differences in \log_{10} freshwater flow for the Clarence (a), Hunter (b) and Hawkesbury (c) River systems between flood and drought events (one-way ANOVA; *P < 0.01; **P < 0.001; d.f. = 17; minimum, 25% quartile, median, 75% quartile and maximum ranges). Note that 1 ML day⁻¹ equals approximately 0.0116 m³ s⁻¹.



Figure 3. Examples of MDS ordination plots revealing detectable contrasts in landings per guild (kg of each guild per month) between flood (**(**) and drought (**(**)) for three adjacent estuarine and coastal systems in eastern Australia. Each point represents a month of flood or drought. See Table 2 for details of estuarine use guilds.

estuarine resident guilds primarily contributed to coastal landings during drought.

Differences in landings per guild between flood and drought were reciprocated in estuarine and coastal systems (Fig. 4). Guilds that dominated estuarine landings during flood subsequently dominated coastal landings during drought. Estuarine migrant and estuarine resident guilds primarily contributed to estuarine landings during flood and coastal landings during drought. Marine estuarine dependent, marine estuarine-opportunist and marine straggler guilds primarily contributed to estuarine landings during drought and coastal landings during flood.

Landings per species

Estuarine and coastal landings per species were significantly different between flood and drought (Tables 4 and 5), with heterogeneity arising from differences in group location (PERMDISP, $P \ge 0.05$). Average dissim-

ilarity in landings per species between flood and drought was relatively high in the Clarence (27.8%), Hunter (25.6%) and Hawkesbury (20.0%) River estuaries. School prawn, Metapenaeus macleavi (Haswell), sea mullet, Mugil cephalus L., and river eels, Anguilla spp., provided the greatest contribution to estuarine landings during flood. Yellowfin bream Acanthopagrus australis (Owen), blue swimmer crab Portunus pelagicus (Rathburn) and whaler sharks Carcharhinus spp. provided the greatest contribution to estuarine landings during drought. Average dissimilarity in landings per species between flood and drought was relatively low in the Clarence (20.1%), Hunter (16.3%) and Hawkesbury (15.4%) coastal systems. School prawn, sea mullet and blue swimmer crab provided the greatest contribution to coastal landings during flood. Yellowfin bream silver biddy Gerres subfasciatus (Cuvier) and yellowtail scad Trachurus novaezelandiae (Richardson) provided the greatest contribution to coastal landings during drought.

Table 4. PERMANOVA of landings, landings per guild, fishing effort, revenue and revenue per guild between flood and drought events in the Clarence (CR), Hunter (HU) and Hawkesbury (HK) River estuaries. Landings (kg of each species per month), landings per guild (kg of each guild per month), fishing effort (days fished per month), revenue (AU\$ for each species per month) and revenue per guild (Australian dollars for each guild per month) were from 27 species groups, 7 estuarine use functional guilds and 10 fishing methods that contributed ≥95% of estuarine fisheries harvest between 1997 and 2007. PERMANOVA models were tested with 4999 random permutations of raw data

Estuary	Fisheries metric	d.f.	MS	Pseudo-F	P (permutation)
CR	Landings	1	502.53	5.4644	0.0006
HU	Landings	1	1119.50	3.4592	0.0050
HK	Landings	1	358.79	2.6866	0.0178
CR	Landings per guild	1	200.12	16.1150	0.0006
HU	Landings per guild	1	715.87	8.0284	0.0002
HK	Landings per guild	1	279.75	4.2633	0.0182
CR	Fishing effort	1	180.68	5.7611	0.0002
HU	Fishing effort	1	1013.20	3.7310	0.0354
HK	Fishing effort	1	125.97	2.8487	0.0216
CR	Revenue	1	483.25	4.9525	0.0004
HU	Revenue	1	1067.50	3.2008	0.0106
HK	Revenue	1	282.17	3.4171	0.0038
CR	Revenue per guild	1	1175.90	7.2485	0.0008
HU	Revenue per guild	1	122.12	3.3717	0.0270
HK	Revenue per guild	1	219.34	2.7927	0.0434

Fishing effort

Detectable contrasts in estuarine and coastal fishing effort were evident between flood and drought (Tables 4 and 5). Heterogeneity in fishing effort between flood and drought arose from differences in the location of groups (PERMDISP, $P \ge 0.05$). Average dissimilarity in fishing effort between flood and drought was relatively high in the Clarence (23.9%), Hunter (19.0%) and Hawkesbury (14.0%) River estuaries. Prawn trawls, prawn set pocket nets and eel traps were primarily used in estuarine systems during flood. Handlines, hauling nets and crab pots were primarily used in estuarine systems during drought. Average dissimilarity in fishing effort between flood and drought was relatively low in the Clarence (9.6%), Hunter (8.3%) and Hawkesbury (6.4%) coastal systems. Fish traps, fish trawls and prawn trawls were primarily used in coastal systems during flood. Handlines, hauling nets and purse seine nets were primarily used in coastal systems during drought.

Revenue per guild

Estuarine and coastal revenue per guild was significantly different between flood and drought (Tables 4

Table 5. PERMANOVA of landings, landings per guild, fishing effort, revenue and revenue per guild between flood and drought events in the Clarence (CRC), Hunter (HUC) and Hawkesbury (HKC) coastal regions. Landings (kg of each species per month), landings per guild (kg of each guild per month), fishing effort (days fished per month), revenue (AU\$ for each species per month) and revenue per guild (Australian dollars for each guild per month) were from 27 species groups, 7 estuarine use functional guilds and 6 fishing methods that contributed ≥95% of coastal fisheries harvest between 1997 and 2007. PERMANOVA models were tested with 4999 random permutations of raw data

Coastal region	Fisheries metric	d.f.	MS	Pseudo-F	P (permutation)
CRC	Landings	1	926.95	7.4754	0.0002
HUC	Landings	1	1068.10	3.3721	0.0310
HKC	Landings	1	1107.90	4.4476	0.0044
CRC	Landings per guild	1	128.49	11.8320	0.0004
HUC	Landings per guild	1	116.43	8.0506	0.0006
HKC	Landings per guild	1	60.59	4.4188	0.0326
CRC	Fishing effort	1	143.60	9.1841	0.0010
HUC	Fishing effort	1	190.20	3.0537	0.0482
HKC	Fishing effort	1	66.83	3.9147	0.0292
CRC	Revenue	1	839.87	8.2163	0.0002
HUC	Revenue	1	535.81	2.8592	0.0270
HKC	Revenue	1	1211.30	4.2372	0.0060
CRC	Revenue per guild	1	373.00	20.4820	0.0002
HUC	Revenue per guild	1	65.93	10.0350	0.0008
НКС	Revenue per guild	1	410.16	6.4192	0.0018

and 5), with heterogeneity arising from differences in group location (PERMDISP, $P \ge 0.05$). Average dissimilarity in revenue per guild was relatively high in the Clarence (22.0%), Hunter (13.24%) and Hawkesbury (9.3%) River estuaries. Estuarine migrant, estuarine resident and catadromous guilds dominated estuarine fisheries revenue during flood. Marine estuarine-opportunist, marine estuarine dependent and marine straggler guilds dominated estuarine fisheries revenue during drought. Average dissimilarity in revenue per guild was relatively low in the Clarence (13.5%), Hunter (9.2%) and Hawkesbury (4.9%) coastal systems. Marine estuarine-opportunist, marine straggler and marine estuarine dependent guilds dominated coastal fisheries revenue during flood. Estuarine migrant and estuarine resident guilds dominated coastal fisheries revenue during drought.

Revenue per species

Significant differences in estuarine and coastal revenue per species were evident between flood and drought (Tables 4 and 5), which resulted from differences in the location of groups (PERMDISP, $P \ge 0.05$). Average



Figure 4. Difference index of landings per guild (kg of each guild per month) between flood and drought calculated using fourth-root transformed data. See Table 2 for details of estuarine use guilds.

dissimilarity in revenue per species was relatively high in the Clarence (27.8%), Hunter (27.2%) and Hawkesbury (20.8%) River estuaries. School prawn, sea mullet and river eels primarily contributed to estuarine fisheries revenue during flood. Yellowfin bream, blue swimmer crab and whaler sharks primarily contributed to estuarine fisheries revenue during drought. Average dissimilarity in revenue per species was relatively low in the Clarence (18.6%), Hunter (16.5%) and Hawkesbury (14.3%) coastal systems. School prawn, sea mullet and blue swimmer crab primarily contributed to coastal fisheries revenue during flood. Yellowfin bream, silver biddy and yellowtail scad primarily contributed to coastal fisheries revenue during drought.

Discussion

Examination of commercial fisheries metrics from three adjacent estuarine and coastal systems revealed the effects of flood and drought events on multispecies, multi-method fisheries. Significant differences in landings, effort and revenue between flood and drought were species, guild and system specific. These differences were caused by heterogeneity in the multivariate location of groups between flood and drought (PERMDISP, $P \ge 0.05$ for all fisheries metrics examined). Similarities in the multivariate patterns of landings and revenue between flood and drought were attributed to limited variation in market price. Variation in the market price per species was relatively small $(C_V = 0.14)$ compared with landings per species $(C_V = 0.57)$ over a 10-year period between 1997 and 2007. Correlations between Bray–Curtis similarity matrices for landings, effort and revenue indicated that multivariate patterns in fisheries metrics represented a signal of ecological response and a function of fishers' harvesting behaviour. Natural variation in freshwater flow modifies the species composition of landings, the temporal and spatial distribution of fishing effort and ultimately the economic performance of commercial fisheries that operate in estuarine and coastal systems (Loneragan & Bunn 1999; Robins *et al.* 2005; Lamberth *et al.* 2009).

The extent that our analysis experienced temporal pseudoreplication (sensu Hurlbert 1984) depends upon the degree of interdependence between the flood and drought events in the three locations examined. As the flood and drought events did not occur at the same time for each location, the three locations are not true replicates of an event. This difficulty of finding true replicated systems is a common issue in analyses of fisheries data (Millar & Anderson 2004). An alternative strategy to avoid pseudoreplication could involve the employment of univariate mixed effects models using an extended time series of hydrological data with increased numbers of flood and drought events. Nevertheless, there are two issues of more importance to the outcomes of this study. Firstly, some of the variability underlying multivariate patterns in fisheries metrics between flood and drought may be related to factors such as bioregion (Pease 1999), estuarine geomorphology (Saintilan 2004), recruitment success (Bennett et al. 1995), fishers' harvesting behaviour (Salas & Gaertner 2004), socio-economics (Charles 1989) and the degree of river regulation within the catchment (Drinkwater & Frank 1994). Secondly, the multivariate patterns identified here are more important than the reported statistical significance. These patterns provide a heuristic model for future studies in alternative systems where some of the statistical constraints experienced here may be less pronounced.

River regulation dampens hydrological extremes and decouples fisheries-flow relationships in eastern Australia (Gillson *et al.* 2009). Our results suggest that river regulation reduces multivariate dispersion in landings, effort and revenue between flood and drought. Pseudo-*F* values obtained from PERMANOVA of landings, effort and revenue between flood and drought were consistently higher for the less regulated Clarence River than the highly regulated Hunter or Hawkesbury Rivers. Deviation in pseudo-*F* values may result from river regulation altering connections between the delivery of freshwater flow and the migration patterns of commercially important species (Drinkwater & Frank 1994). The effects of flood and drought events on fisheries resources are likely to be more clearly manifested in estuarine and coastal systems that receive freshwater from rivers with a relatively low degree of regulation and high variability in freshwater flow.

Landings composition between flood and drought

Flood and drought events were associated with shifts in the species composition of landings. Estuarine migrant species (e.g. school prawn and sea mullet) primarily contributed to landings during flood, whilst marine estuarine-opportunist species (e.g. vellowfin bream and blue swimmer crab) primarily contributed to landings during drought. Freshwater flow influences the distribution and abundance of fish and invertebrates due to salinity fluctuations altering habitat availability (Jassby et al. 1995; Kimmerer 2002; Barletta et al. 2005). Differences in the salinity tolerance of eurvhaline and stenohaline species may be attributed to observed disparity in the responses of coastal biota to flood and drought (Cognetti & Maltagliati 2000). The school prawn is a euryhaline species that responds to flood events and resultant reductions in salinity by emigrating from estuarine to coastal systems (Ruello 1973; Glaister 1978; Dall et al. 1990). Floodwaters reduce salinity on the continental shelf, expanding the offshore estuary and permitting euryhaline species to increase their distribution into coastal habitats (Able 2005). Droughts can induce seaward migration in euryhaline species due to increased salinity creating hypersaline conditions, thereby reducing the extent of available habitat for fish and invertebrates in estuaries (Dolbeth et al. 2008). Marine stenohaline species are transient components of estuarine communities because of stenotopic environmental requirements (Whitfield 1994). Floods result in the decreased estuarine abundance of marine stenohaline species because of lower salinity forcing the seaward displacement of preferred habitat (Marais 1983; Ter Morshuizen et al. 1996; Whitfield & Harrison 2003). Droughts, alternatively, may create windows of opportunity for marine stenohaline species to enter estuaries because of increased salinity (Nordlie 2003). Silver biddy is a marine stenohaline species that may immigrate into estuaries during drought because of increased salinity expanding available habitat.

Flood waters can flush estuarine resident species out of estuaries into coastal systems (Strydom *et al.* 2002). Nevertheless, estuarine resident species (e.g. trumpeter whiting *Sillago maculata* Quoy and Gaimard) primarily contributed to coastal landings during drought. Trumpeter whiting may retreat to coastal systems during drought, and therefore this species may have been more appropriately described as an estuarine migrant. Support for downstream displacement by flooding was provided for catadromous species (e.g. anguillid eels), which primarily contributed to estuarine landings during flood. Anguillid eels can be washed out of rivers into estuaries by flood events (Tsukamoto & Arai 2001).

Resistance and resilience of aquatic biota to flood and drought events may be facilitated by movement to refugia (Lake 2007). Aquatic organisms possess chemosensory organs that enable detection and orientation towards suitable ambient conditions (Weissburg 2000). We observed that flood dispersal and migration is strongly influenced by freshwater flow altering estuarine salinity regimes (Garcia et al. 2003, 2004; Sosa-López et al. 2007). We observed that flood and drought events altered landings composition by modifying species exchange between estuarine and coastal systems. Flood and drought events may result in shifts in the species composition of landings by modifying rates of estuarine immigration and emigration due to salinity fluctuations altering habitat availability. Temporal and spatial variation in freshwater flow modifies salinity regimes forcing the composition of coastal fish communities to oscillate through a continuum of successionary states (Garcia et al. 2001; Whitfield 2005; Love et al. 2009).

Species-specific landings between flood and drought

Significant differences in estuarine and coastal landings between flood and drought were likely to result from alterations in catchability. Freshwater flow influences the catchability of fish and invertebrates by modifying their distribution due to changes in salinity and/or turbidity (Loneragan & Bunn 1999). School prawns primarily contributed to estuarine and coastal landings during flood. Flood events result in the increased catchability of school prawns due to reductions in salinity enhancing emigration rates from estuarine to coastal systems (Racek 1959; Ruello 1973; Glaister 1978). Freshwater flow also has a marked influence on the catchability of sea mullet due to changes in salinity stimulating migration and schooling into preferred habitat (Gillson et al. 2009). Salinity strongly influences habitat selection by sea mullet, with individuals locating optimum salinity conditions to minimise osmoregulatory costs and maximise growth rates (Cardona 2000, 2006; Chang et al. 2004). Sea mullet dominated fisheries harvest (\geq 35%) providing the greatest contribution to significant differences in estuarine and coastal landings between flood and drought. River eels primarily contributed to estuarine landings during flood. High flows stimulate seaward migration in river eels, thereby increasing their catchability in estuaries (Chen *et al.* 1994; Miyai *et al.* 2004; Tsukamoto 2009).

Increased freshwater flow forces the emigration of blue swimmer crab from estuarine to coastal systems (Potter et al. 1983). Blue swimmer crab primarily contributed to estuarine landings during drought and coastal landings during flood. Salinity exerts a profound influence on the spatial distribution of blue swimmer crab, with individuals preferring salinities > 20 (Potter et al. 1983; Potter & de Lestang 2000; de Lestang et al. 2003). Differences in estuarine and coastal landings of blue swimmer crab between flood and drought may result from alterations in catchability due to individuals shifting their spatial distribution to seek optimal salinities. Yellowfin bream primarily contributed to coastal landings during drought. Drought results in the increased catchability of yellowfin bream because of increased estuarine salinity stimulating downstream migration into coastal habitats (Gillson et al. 2009).

Another possible mechanism underlying differences in species-specific landings between flood and drought is alterations to the catchability of fish and invertebrates that result from changes in turbidity (Loneragan & Bunn 1999; North & Houde 2003; Robins et al. 2005). Changes in turbidity strongly influence the catchability of fish and invertebrates by modifying their distribution and abundance due to alterations in habitat availability (Cyrus & Blaber 1987, 1992; Grange et al. 2000). Silver biddy, for example, primarily contributed to estuarine and coastal landings during drought. Drought events may result in the increased catchability of silver biddy because of higher salinity and/or lower turbidity increasing habitat availability in estuarine and coastal systems. Flood and drought events, therefore, may alter the catchability of coastal species by stimulating migration and schooling due to changes in salinity and/or turbidity altering habitat availability.

Fishers' harvesting behaviour between flood and drought

Fishers employ dynamic fishing strategies as an adaptive response to alterations in resource abundance and environmental conditions (Salas & Gaertner 2004). We observed that fishers' modified harvesting behaviour between flood and drought events. Prawn trawls and prawn set pocket nets were primarily used during floods, which resulted in increased landings of school prawns. The mass movement of school prawns from estuarine to coastal systems after flooding noticeably increases the susceptibility of this species to fishing effort (Glaister 1978). Commercial fishers recognise that increased freshwater flow results in increased landings of penaeid prawns because of extensive practical experience. Prawn trawls dominated fishing effort (\geq 35%) providing the greatest contribution to significant differences in harvesting behaviour between flood and drought. Eel traps were primarily used during flood, which accounts for increased estuarine landings of river eels. Handlines, hauling nets and crab pots were primarily used in estuaries during drought, which can be attributed to fishers targeting the increased catchability of yellowfin bream, blue swimmer crab and whaler sharks. Flood and drought events may prompt fishers to adjust their harvesting behaviour by altering fishing method use. Handlines, hauling nets and purse seine nets were primarily used in coastal systems during drought, which explains increased coastal landings of yellowfin bream, silver biddy and yellowtail scad. Accordingly, these results suggest that fishers' modify their harvesting behaviour to exploit alterations to the catchability of coastal species that arise during flood and drought.

Revenue between flood and drought

Environmental fluctuations influence the economic productivity of commercial fisheries by modifying the availability of fisheries resources (Grafton *et al.* 2006). Significant differences in fisheries revenue between flood and drought were primarily attributed to variation in landings rather than market price. Landings of high-value estuarine migrant species (e.g. school prawn) primarily contributed to revenue during flood, whilst landings of low-value marine estuarine-opportunist species (e.g. silver biddy) primarily contributed to revenue during drought. Flood and drought events, therefore, may regulate revenue generation in estuarine and coastal fisheries by modifying the species composition of landings.

Results from this study indicate that flood and drought events redistributed fisheries resources between estuarine and coastal systems, modifying the bioeconomic productivity of commercial fisheries. Flood and drought events may influence the bioeconomic productivity of commercial fisheries by modifying the species composition of landings, fishers' harvesting behaviour and revenue generation. Coastal species that exhibit

varying degrees of estuarine dependency are influenced by variation in freshwater flow (Lamberth et al. 2009). Differences in landings and revenue between flood and drought were most discernible for estuarine migrant (e.g. school prawn and sea mullet) and marine estuarine-opportunist (e.g. yellowfin bream and blue swimmer crab) species. With increased climatic variability and greater hydrological extremes predicted in many regions of the world (Alley et al. 2003), improved knowledge of the effects of flood and drought events on multi-species and multi-method fisheries is essential to devise effective management strategies. Future research would be most profitably directed on examining how individual fishers, rather than the industry in aggregate, modify their harvesting behaviour during flood and drought events. Understanding variation in the harvesting behaviour of individual fishers during flood and drought would provide insight into patterns of fishing method use that will make fishing businesses more robust to climate change.

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