

**Freshwater flow and fisheries production in estuarine and coastal
systems: where a drop of rain is not lost**

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- July 2011
- [Reviews in Fisheries Science](#) 19(3):168-186

DOI: [10.1080/10641262.2011.560690](https://doi.org/10.1080/10641262.2011.560690)

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Date: 27 January 2011

Version: 1

File name: Gillson 2010

Word count: 7375

Target journal: Reviews in Fisheries Science

Abstract

This review presents a synopsis of the impacts of freshwater flow on fisheries production in estuarine and coastal systems, with particular emphasis on regional examples from eastern Australia and southern Africa. Freshwater flow impacts habitat availability, trophic interactions and fishers' harvesting behaviour in estuarine and coastal systems. Seasonal and interannual variation in freshwater flow influences the distribution and abundance of fish and invertebrates through changes in growth, survival and recruitment. Episodic flood and drought events have pronounced impacts on fisheries production due to rapid changes in physicochemical conditions modifying species richness and diversity. Many documented reductions in fisheries production have been attributed to river regulation modifying natural variation in freshwater flow. Protecting natural flow regimes is likely to be an effective management strategy to maintain the production of estuarine and coastal fisheries. Understanding the freshwater requirements of estuarine and coastal fisheries will become increasingly important as climate change modifies the hydrological cycle and human population growth increases demand for water resources. One major challenge for scientists seeking to explore relationships between freshwater flow and fisheries production is to understand how variable flows influence resource availability, fishing activity and the economic performance of commercial fisheries in estuarine and coastal systems.

Keywords: Freshwater flow; Fisheries production; River regulation; Climate change

Introduction

Not a single drop of water received from rain should be allowed to escape into the sea without being utilised for human benefit — Parākramābāhu, the Great Sinhalese King of Sri Lanka, 1153-1186

Most fisheries production worldwide is associated with three nutrient enrichment processes: coastal upwelling, tidal mixing and land-based runoff including major river outflow (Caddy and Bakun 1994). Natural variation in freshwater flowing from rivers strongly influences the production of fish, crustaceans and molluscs in estuarine and coastal fisheries (Beamish et al. 1994; Grimes 2001; Erzini 2005). Despite consistent links between freshwater flow and the production of estuarine and coastal fisheries, underlying mechanisms remain poorly understood. Proposed mechanisms include: (1) improved growth and survival due to nutrient enrichment increasing primary and secondary production (Darnaude 2005); (2) alterations to abundance resulting from salinity fluctuations modifying habitat availability (Kimmerer 2002a); (3) changes to migration and schooling altering catchability (Loneragan and Bunn 1999); (4) increased estuarine immigration owing to changes in offshore olfactory concentration gradients from riverine plume fronts (Whitfield 1994); and (5) recruitment variability arising from alterations to water physicochemistry (North and Houde 2003). These mechanisms are interrelated, operating over different temporal and spatial scales, and therefore no single characteristic of freshwater flow is likely to be solely responsible for influencing fisheries production in estuarine and coastal systems.

Freshwater flow is critical landscape process that has profound effects on the physical, chemical and biological properties of estuarine and coastal systems (Skreslet 1986). Seasonal and interannual variation in freshwater flow is essential for maintaining the structure and function of estuarine and coastal systems (Schlacher and Wooldridge 1996; Sklar and Browder 1998; Young and Potter 2002). Nevertheless, there is still a false perception that freshwater is 'lost' when it enters estuarine or coastal systems (Gillanders and Kingsford 2002). Growing demand for freshwater resources has necessitated the construction of large dams and inter-basin transfer schemes often with little regard for impacts on estuarine and coastal fisheries (Walker 1985; Loneragan and Bunn 1999; Erzini 2005). When river regulation has modified natural variation in the flow regime, major declines in the production of estuarine and coastal fisheries have followed (Drinkwater and Frank 1994). Modified flow regimes have diminished the abundance of fish and invertebrates in estuarine and coastal systems, which has forced commercial fishers to exploit stocks further offshore (Roberts 2007).

A comprehensive literature search identified more than 800 published articles examining the impacts of freshwater flow (or rainfall) on fishery-related topics in estuarine and coastal systems (Figure 1). Most of these articles (82%) focused on the ecological impacts of variation in freshwater flow on fish and invertebrates. In contrast, the economic impacts of variable flows on commercial fisheries have received relatively little attention. The aim of this review is to present a synopsis of the ecological and socio-economic impacts of freshwater flow on estuarine and coastal fisheries. Examples from temperate, tropical and subtropical regions are used to illustrate connections between freshwater flow and the life histories of fish and invertebrates in estuarine and coastal systems. Regional examples from eastern

Australia and southern Africa have been given particular emphasis because rivers in these areas exhibit the most variable flows in the world (Figure 2), which provides an ideal opportunity to extrapolate the impacts of freshwater flow on the production of estuarine and coastal fisheries.

Nature of freshwater flows

Freshwater flow regimes are often related to latitude (Finlayson (Finlayson and McMahon 1988; Kench 1999; Poff et al. 2006). Rivers at high latitudes exhibit relatively consistent flows but seasonal peaks typically follow melting of snow or glaciers (Walker 1985). Snowmelt from mountainous regions triggers peak flows in spring or summer in some areas of the world (e.g. Canada: Smith 2000), but snowmelt is not an important factor influencing flows in most Australian and southern African rivers (Finlayson and McMahon 1988). Flows at mid and low latitudes are relatively stochastic and less predictable (Walker 1985; Puckridge et al. 1998; Thoms and Sheldon 2000). Rivers in Australia and southern Africa exhibit extreme hydrological conditions characterised by the most variable flows in the world (Peel et al. 2004). Annual variation in freshwater flow from Australian ($C_V = 0.84$) and southern African ($C_V = 0.73$) rivers exceeds the world average ($C_V = 0.40$) by a factor of more than $\times 1.8$ (Finlayson and McMahon 1988). Sporadic rainfall events generate stochastic river flows in these regions (Dettinger and Diaz 2000). In eastern Australia, rivers are influenced by alternating flood and drought dominated regimes (Erskine and Warner 1998), with freshwater primarily delivered into estuarine and coastal systems by episodic flow events (Eyre 1998).

Climatic variability influences the quantity of freshwater entering estuarine and coastal systems by altering rainfall and evaporation rates. Teleconnection patterns are atmospheric circulation systems that influence climatic conditions over vast geographic areas (Barnston and Livezey 1987). One of the most prominent teleconnection patterns is the North Atlantic Oscillation (NAO) in the Northern Hemisphere (Rogers 1984; Hurrell 1995; Hurrell et al. 2003). The NAO is a driving force of climatic systems that strongly influences rainfall, air temperature and river flow (Hurrell and Van Loon 1997; McHugh and Rogers 2001; Rîmbu et al. 2002). Another prominent teleconnection pattern is the El Niño Southern Oscillation (ENSO), which exerts a profound influence on rainfall, air temperature and river flow in the Southern Hemisphere (Kuhnel et al. 1990; Molles and Dahm 1990; Allan et al. 1996). Rainfall in Australia and southern Africa are also related to sea surface temperature oscillations in the Central Pacific (Power et al. 1999; Reason and Rouault 2002) and the Indian Ocean (Landman and Mason 1999; Ashok et al. 2003).

Once freshwater enters estuarine and coastal systems, its influence on environmental conditions depends on tidal regimes, wind direction and strength, estuary mouth topography and the nature of ocean currents. Freshwater flow influences a myriad of environmental factors in estuarine and coastal systems including: estuary channel dimensions (Reddering 1988), the status of an estuary mouth (Roy et al. 2001), the offshore extent of riverine plume fronts (Grimes and Kingsford 1996), tidal mixing (Hunter et al. 2010), water temperature (Attrill and Power 2002), salinity regimes (Kurup et al. 1998), dissolved oxygen concentrations (Somville and De Pauw 1982), nutrient inputs (Qu and Kroeze 2010), sediment delivery (Eyre 1998), turbidity

(Laheta and Stramski 2010), stratification (Schumann and Pearce 1997) and the residence time of pollutants (Baird and Heymans 1996).

Anthropogenic modification of freshwater flow

Relatively few modern-day rivers have retained their natural flow regime (Poff et al. 1997). River headwaters have been diverted, middle reaches dammed and floodplains developed (Boon 1992). Concern has been expressed about the impacts of modifying the delivery of freshwater flow into estuarine and coastal systems (Benson 1981; Whitfield and Wooldridge 1994; Sklar and Browder 1998). River regulation disrupts the structure and function of estuarine and coastal systems by forcing physicochemical processes to deviate from natural successional patterns (Sklar and Browder 1998; Gillanders and Kingsford 2002; Sheaves et al. 2007). Anthropogenic modification of freshwater flow alters sediment delivery (Eyre 1998), erosion processes (Roy 1984), riverine plume fronts (Grimes and Kingsford 1996), nutrient inputs (Sin et al. 1999), salinity regimes (Sklar and Browder 1998) and dissolved oxygen concentrations (Serafy et al. 1997). These alterations to physicochemical processes can have deleterious effects on fish and invertebrates by degrading habitat and restructuring food webs in estuarine and coastal systems (Pollard and Hannan 1994; Baird and Heymans 1996; Adams et al. 2009).

Aquatic species have evolved life history strategies in direct response to natural flow regimes (Bunn and Arthington 2002). Modification of freshwater flow impacts the distribution, abundance and species composition of fish and invertebrates in estuarine and coastal systems (Drinkwater and Frank 1994). Impacts are most pronounced for

anadromous species that require longitudinal and lateral connectivity between marine and freshwater habitats to migrate into riverine spawning grounds. On the Pacific coast of North America, for example, more than 75% of the original 2500 km of spawning and rearing habitat for chinook salmon (*Oncorhynchus tshawytscha*) has been eliminated due to the construction of an extensive network of hydroelectric dams in the Columbia River basin (Dauble and Geist 2000). In south-eastern Australia, stream impoundments have obstructed almost half of the aquatic habitat for migratory fish in coastal drainages (Harris 1984). Habitat destruction due to modified flow regimes can remove environmental cues required for migration (Zale and Adornato 1996), lower species diversity (Plumstead 1990) and create inimical conditions for native biota favouring the colonisation of exotic species (Bunn and Arthington 2002). Protecting natural flow regimes is an essential requirement for the conservation of estuarine and coastal systems (Sklar and Browder 1998; Grange et al. 2000; Whitfield and Taylor 2009).

Commercial fisheries are under increasing threat from river regulation modifying the delivery of freshwater into estuarine and coastal systems. Numerous examples of the major, irreversible impacts of river regulation on commercial fisheries exist worldwide (e.g. the Mediterranean Sea: Aleem 1972; the Gulf of Mexico: Sklar and Browder 1998 and the Caribbean Sea: Baisre and Arboleya 2006). A striking example of the consequences of modifying the delivery of freshwater into estuarine and coastal systems has been provided by the construction of the Aswan High Dam in the Mediterranean Nile delta (Bebars and Lasserre 1983). After the construction of the High Aswan Dam in 1969, freshwater flow from the Nile River decreased by 90% resulting in a loss of primary production and a consequent ~80% reduction in

Egyptian fishery landings in the Mediterranean coastal region. Declines in landings were primarily from economically valuable sardine (Wadie 1982) and (Bishara (Bishara 1984) fisheries.

Relationships between freshwater flow and fisheries production

Commercially harvested fish and invertebrates that exhibit varying degrees of estuarine dependency are influenced by variation in freshwater flow. Relationships between freshwater flow and the landings of more than 80 estuarine or coastal fishery species have been reported worldwide (examples shown in Table 1). Commercial landings of fish, crustaceans and molluscs have been related to variation in freshwater flow in temperate, tropical and sub-tropical regions. Relationships between freshwater flow and landings can be positive, negative or inconsistent among regions for the same species (Figure 3). For example, positive relationships between freshwater flow and landings of fish and invertebrates were reported in tropical northern Australia (Loneragan and Bunn 1999). Negative relationships between freshwater flow and landings of Róbalo (*Eleginops maclovinus*) were documented in subtropical central-south Chile (Quiñones and Montes 2001); and positive and negative relationships between freshwater flow and landings of dusky flathead (*Platycephalus fuscus*) were identified in temperate eastern Australia (Gillson et al. 2009). Some of the variability underlying relationships between freshwater flow and landings of fish and invertebrates may be related to factors such as geographic location (Gillanders and Kingsford 2002), estuarine geomorphology (Saintilan 2004), degree of river regulation within the surrounding catchment (Drinkwater and Frank 1994) and the life history of individual species (Robins et al. 2005).

Freshwater flow has profound effects on the early-life history stages of marine fish. For example, seasonal variation in freshwater flow influences the abundance, growth and mortality of age-0 red drum (*Sciaenops ocellatus*), pinfish (*Lagodon rhomboides*), sand seatrout (*Cynoscion arenarius*) and spot (*Leiostomus xanthurus*) in the Suwannee River estuary, North America (Purtlebaugh and Allen 2010). Natural variation in freshwater flow regulates recruitment by modifying the distribution, growth and mortality of juvenile marine fish (Kimmerer et al. 2001; North and Houde 2003; Staunton-Smith et al. 2004). Riverine plume fronts that extend offshore are sites of intense biological activity that favourably influence the recruitment and survival of juvenile marine fish (Grimes and Kingsford 1996). Off the Bay of Biscay, for example, the spatial extent of the riverine plume front influences the production of juvenile sole (*Solea solea*) by determining the availability of estuarine nursery grounds (Le Pape et al. 2003). Large riverine plume fronts increase offshore concentrations of land-based cues that stimulate marine fish to migrate from coastal spawning grounds towards estuaries (James et al. 2007; Vinagre et al. 2007; Vinagre et al. 2009).

Seasonal and interannual variation in freshwater flow influences the growth rates of fish and invertebrates. For example, high flows enhance the growth of barramundi (*Lates calcarifer*) in eastern Australia (Robins et al. 2006), and reduce the growth of Gulf menhaden (*Brevoortia patronus*) in North America (Deegan 1990). Freshwater flow influences growth rates by modifying food availability, salinity regimes and water temperature in estuarine and coastal systems (Loneragan and Bunn 1999; Robins et al. 2005; Shoji et al. 2006). Positive relationships between freshwater flow

and the growth rates of school prawns (*Metapenaeus macleayi*) were attributed to increased food availability and decreased salinity in the Hunter River estuary on the east coast of Australia (Ruello 1973). Experimental studies have shown that the food-unlimited growth rates of penaeid prawns function most efficiently within relatively narrow temperature-salinity ranges (O'Brien 1994; Kumlu et al. 2000; Su et al. 2010). Under laboratory conditions, for instance, banana prawns (*Penaeus merguensis*) grow fastest at temperatures between 20-31°C and in salinities between 20-30‰ (Staples and Heales 1991). Freshwater flow has a particularly pronounced effect on the growth of sessile mollusc species. Negative relationships between freshwater flow and the growth rates of eastern oysters (*Crassostrea virginica*) result from suboptimal low salinities (mean ≤ 17 ppt) in North America (Wilber 1992; Livingston et al. 2000; Wang et al. 2008).

Natural fluxes in the flow regime influence the catchability of fish and invertebrates by restricting their distribution or stimulating movement into areas where they are more likely to be caught (Loneragan and Bunn 1999). Freshwater effects on catchability are most noticeable for short-lived schooling species such as penaeid prawns. For example, high flows result in the increased catchability of school prawns due to reductions in salinity enhancing emigration rates from estuarine to coastal systems in eastern Australia (Racek 1959; Ruello 1973; Glaister 1978). Freshwater flow also has a pivotal role in determining the catchability of longer-lived, migratory fish species. For instance, freshwater flow alters the catchability of sea mullet (*Mugil cephalus*) in estuaries by stimulating migration and schooling due to salinity fluctuations altering habitat availability in eastern Australia (Gillson et al. 2009). Seasonal pulses of freshwater proximate to reproductive periods strongly influence

catchability by stimulating spawning migrations in estuarine-dependent fish. For example, increased freshwater flow into the Princess Charlotte Bay of eastern Australia results in the increased the catchability of barramundi by stimulating mature males to migrate towards estuarine spawning grounds at the beginning of the wet season (Balston 2009).

Freshwater flow has a controlling influence on fisheries production by regulating habitat availability, trophic interactions and fishers' harvesting behaviour in estuarine and coastal systems (Figure 4). Seasonal and interannual variation in freshwater flow modifies environmental conditions, stimulating a biological response and forcing commercial fishers to alter their fishing activity in estuarine and coastal systems.

Habitat availability

Natural variation in freshwater flow directly impacts fisheries production by regulating environmental factors that determine habitat availability for fish and invertebrates. Biotic effects stem from four main environmental factors forced by variation in freshwater flow: modified rates of sediment delivery; salinity fluctuations; turbidity changes; and thermal alteration.

Temporal and spatial variation in freshwater flow controls the duration and frequency that an estuary mouth is open or closed by modifying rates of sediment delivery (Reddering and Rust 1990; Eyre 1998). The status of an estuary mouth influences the distribution, abundance and species composition of fish and invertebrate communities (Whitfield and Kok 1992; Vorwerk et al. 2003; Vivier and Cyrus 2009). Permanently

open estuaries maintain a constant connection with the sea, thus enabling fish and invertebrate migrations between estuarine and coastal systems (Kok and Whitfield 1986; Potter et al. 1990; Whitfield 1994). Temporary mouth closure, however, inhibits species exchange resulting in the decreased abundance of marine taxa, recruitment limitation and a loss of estuarine nursery function (Wooldridge 1991; Harrison and Whitfield 1995; Young and Potter 2002). Prolonged mouth closure can result in extensive fish mortalities due to changes in salinity creating osmoregulatory stress. For example, prolonged closure of the Bot Estuary in southern Africa resulted in the mortality of more than 7000 fish from 9 species due to salinities lower than 3‰ producing oligohaline conditions (Bennett 1985). Similarly, prolonged closure of the Seekoei Estuary in southern Africa resulted in the mortality of more than 6000 fish from 11 species due to salinities higher than 95‰ producing hypersaline conditions (Whitfield 1989).

Freshwater flow has a profound effect on community composition in estuarine and coastal systems by altering the distribution and abundance of marine, estuarine and freshwater species due to changes in salinity (Jassby et al. 1995; Hurst et al. 2004; Costa et al. 2007). One of the most essential adaptations of organisms that enter estuaries is the ability to adjust to changes in salinity (Panikkar 1960). Salinity strongly influences habitat selection, with species actively seeking optimum habitat conditions to minimise osmoregulatory costs and maximise growth rates (Edeline (Edeline et al. 2005; Cardona 2006; Shen et al. 2009). Differences in the salinity tolerance of euryhaline and stenohaline species are often attributed to the divergent responses of estuarine and coastal biota to variation in freshwater flow. Freshwater encroachment onto the continental shelf lowers salinity, expands estuarine conditions

offshore and permits euryhaline species to increase their distribution into coastal waters (Able 2005). Marine stenohaline species respond to increased freshwater flow by emigrating from estuarine into coastal systems due to lower salinity forcing the seaward displacement of habitat (Kimmerer 2002a; Whitfield and Harrison 2003; James et al. 2007). The influence of freshwater flow on salinity is particularly important for early-life history stages of fish in estuarine nursery grounds (Kimmerer et al. 2001; North and Houde 2003; Bolle et al. 2009). For example, freshwater flow influences the distribution of black bream (*Acanthopagrus butcheri*) eggs and larvae by altering salt-wedge position and halocline depth in the Glenelg and Hopkins estuaries on the east coast of Australia (Nicholson et al. 2008). A combination of intermediate flows ($> \sim 3000 \text{ ML d}^{-1}$) and strong vertical salinity stratification have also been shown to favourably influence the recruitment of black bream by increasing the availability of spawning habitat in Gippsland Lakes, eastern Australia (Jenkins et al. 2010).

Freshwater flow can modify the distribution and abundance of marine fish by altering turbidity levels in estuarine and coastal systems (Cyrus and Blaber 1992; Blaber et al. 1995; Grange et al. 2000). Turbidity has a profound effect on the early-life history stages of marine fish (Blaber and Blaber 1980; Whitfield 1994; Harris et al. 2001). Detailed studies in KwaZulu-Natal estuaries on the east coast of southern Africa have demonstrated that juvenile marine fish can be divided into categories depending on the turbidity preference of individual species (Cyrus and Blaber 1987a; 1987b). Cyrus and Blaber (1987c) identified that 16 out of 20 species studied exhibited a preference for turbid waters. Offshore turbidity gradients influence the feeding rates of fish, predation pressure and larval immigration into estuaries (Blaber and Blaber 1980;

Hecht and van der Lingen 1992; Utne-Palm 2002). Annual changes in freshwater flow into Chesapeake Bay on the east coast of North America control the survival and recruitment of anadromous fish by modifying the co-occurrence of larvae and predators in the high turbidity refuge (North and Houde 2003). Rapid increases in turbidity due to sudden influxes of freshwater can impair estuarine nursery function leading to increased larval mortality and decreased prey availability (Gonzalez-Ortegon et al. 2010).

Fisheries production is strongly influenced by freshwater flow altering water temperature in estuarine and coastal systems. For example, high flows and warm sea surface temperatures enhance salmon production in the North Pacific Ocean (Mantua et al. 1997). Temperature is an ecological resource that controls the metabolic rate and physiology of fish (Magnuson et al. 1979). Fish can be assigned a thermal niche according to the temperature preference of individual species (Magnuson and Destasio 1996). Habitat selection by juvenile marine fish is dependent on the availability of optimal thermal habitats in estuarine and coastal systems (Attrill and Power 2002; 2004). Freshwater flow and water temperature synergistically impact fish community structure. For instance, winter water temperature and freshwater flow were the most important environmental factors explaining the distribution and abundance of anadromous and coastal spawning species in the nursery grounds of Chesapeake Bay, North America (Wingate and Secor 2008).

One of the major difficulties in isolating mechanisms underlying relationships between freshwater flow and fisheries production is that river flow impacts a myriad of environmental factors that determine the habitat characteristics of estuarine and

coastal systems. In central Mozambique, for example, positive relationships between Zambezi River flow and landings of white shrimp (*Penaeus indicus*) were attributed to lower salinities increasing available habitat for recruitment, elevated turbidity providing refuge from predators and floodwaters increasing larval dispersal in estuarine nursery grounds (Gammelsrød 1992). Another difficulty is that the direction of the relationship between freshwater flow and fisheries production can be attributed to differences in the physicochemical preference of individual species. For instance, the catch rates of 30 out of 45 fish species were related to differences in turbidity and salinity preference in the Emberly estuary in northern Australia (Cyrus and Blaber 1992).

Trophic interactions

Freshwater flow can also indirectly impact fisheries production via a trophic cascade. Natural variation in freshwater flow regulates fisheries production by altering the delivery of terrestrially-derived nutrients and organic matter into estuarine and coastal systems (Darnaude 2005). Nutrient-enriched freshwater stimulates increased primary and secondary production (Mallin et al. 1993; Sin et al. 1999; Scharler and Baird 2005), which is then propagated through the food web to species occupying higher trophic levels (Livingston et al. 1997; Salen-Picard et al. 2002; Connolly et al. 2009). Pulses of freshwater and associated nutrient inputs elevate phytoplankton and zooplankton abundance enhancing the recruitment, growth and survival of fish and invertebrates (Quiñones and Montes 2001; Hoffman et al. 2007; KostECKI et al. 2010).

Estuarine and coastal food web structure is highly sensitive to variation in freshwater flow (Darnaude 2005). Seasonal and interannual variation in freshwater flow determines the origin of carbon assimilated into pelagic and benthic food webs (Canuel et al. 1995; Vorwerk and Froneman 2009; Vinagre et al. 2010). Relationships between nutrient-enriched freshwater and fisheries production depend on how reliant a food web is on river flow to supply nutrients and organic matter. A trophic-driven mechanism for fisheries production is particularly important in oligotrophic or semi-enclosed coastal regions that receive limited nutrient supplies from oceanic currents and upwelling events (e.g. the Gulf of Mexico: Wissel and Fry 2005; the Mediterranean Sea: Darnaude et al. 2005; and the South China Sea: Qiu et al. 2010). Nutrient-enriched freshwater, however, may not always have such an important role in determining fisheries production. Kimmerer (2002a) demonstrated that variation in the abundance and survival of organisms at higher trophic levels in the San Francisco estuary resulted from freshwater flow altering habitat availability rather than trophic dynamics. Upward trophic transfer was an unlikely mechanism in this estuary given that the positive flow responses of taxa in higher trophic levels (e.g. fish and shrimp) were largely uncoupled from the inconsistent flow responses of taxa in lower trophic levels (e.g. phytoplankton and zooplankton).

Stable isotope analysis has provided insight into how nutrient-enriched freshwater contributes to the energetic requirements of commercially harvested fish and invertebrates. Darnaude et al. (2004) used stable isotope analysis to link flow-related increases in polychaete abundance to the increased growth and survival of sole, confirming previously reported claims of relationships between freshwater flow and fisheries production in the oligotrophic northwest Mediterranean basin (Salen-Picard

et al. 2002). We can expect that the increased use of stable isotopes will improve our understanding of how nutrient-enriched freshwater influences fisheries production, particularly in the estuarine and coastal systems of eastern Australia and southern Africa that experience highly variable flow regimes.

Harvesting behaviour

Freshwater flow can indirectly impact fisheries production by altering the harvesting behaviour of commercial fishers in estuarine and coastal systems. Off the east coast of Australia, for example, commercial fishers respond to variable flows by modifying their harvesting behaviour to opportunistically exploit alterations to the catchability of fishery species (Gillson et al. under review). Adjustments to harvesting behaviour enable fishers' to exploit the increased catchability of estuarine migrant species (e.g. school prawn) during periods of flood and marine estuarine-opportunist species (e.g. blue swimmer crab, *Portunus pelagicus*) during periods of drought. Fisheries scientists must recognise that relationships between freshwater flow and fisheries production represent a signal that is a mixture of ecological response and fishers' harvesting behaviour. Fishing activity in estuarine and coastal systems is influenced by variation in freshwater flow (Loneragan and Bunn 1999; Moses et al. 2002; Lamberth et al. 2009). When freshwater flow alters the availability of fisheries resources, commercial fishers respond by modifying their harvesting behaviour to minimise fishing effort and maximise catch rates. Nevertheless, relatively few of the identified articles (8%) referred to the impacts of freshwater flow on fishing activity. More information on how variable flows influence fishers' harvesting behaviour is required to better understand the impacts of freshwater flow on fisheries production.

Episodic flow events

Freshwater flow *per se* may not be as important in determining fisheries production as episodic flow events (Gillson et al. 2009). Floods and droughts are episodic flow events that maintain and enhance biological productivity in estuarine and coastal systems (Flint 1985; Martin et al. 1992; Dolbeth et al. 2008). Along the eastern Australia coastline, for example, fish communities and dependent fisheries are affected by the flood-drought cycle (Loneragan and Bunn 1999; Robins et al. 2005; Ives et al. 2009). Estuarine migrant species primarily contribute to landings during flood, while marine estuarine-opportunist species primarily contribute to landings during drought (Figure 5). Flood and drought events modify the species composition of landings by altering rates of estuarine immigration and emigration due to changes in salinity altering habitat availability.

Flood events temporary reduce species abundance and diversity in estuaries.

Excessive delivery of freshwater into southern African estuaries can decrease fish abundance by forcing marine taxa to emigrate from estuarine into coastal systems due to rapid declines in salinity (Marais 1983; Ter Morshuizen et al. 1996; Whitfield and Harrison 2003). Floods create a physical barrier to the recruitment of marine taxa by lowering salinity, reducing available nursery habitat and forcing the seaward dispersion of larvae (Loneragan and Bunn 1999; Strydom et al. 2002; Whitfield and Harrison 2003). Estuarine food web structure can be disrupted by floodwaters altering the availability of pelagic and benthic food resources (Vinagre et al. 2010). Severe floods carrying large quantities of suspended sediment can be lethal to estuarine biota.

For example, a major flash flood into the Sundays River Estuary on the east coast of southern Africa resulted in extensive mortalities of marine migrant and estuarine resident species due to suspended sediment clogging gills, low salinities creating osmoregulatory stress and reduced dissolved oxygen levels causing asphyxiation (Whitfield and Paterson 1995). Post-flood reductions in abundance are most pronounced for sessile bivalve species that cannot actively avoid suspended sediment clogging feeding structures (Cardoso et al. 2008). Flood generated mass mortalities of fish result from the production of unfavourable water quality characteristics in estuarine and coastal systems. An excellent example of this has been provided by severe flood events that caused widespread mortalities of fish in the Richmond, Clarence and Mcleay River estuaries in eastern Australia (Dawson 2002; Eyre et al. 2006; Kroon and Ludwig 2010). Floodwaters reduced dissolved oxygen concentrations to lethal limits for fish ($\leq 1\text{mg/L}$) by flushing decomposing organic matter and acidified water from the surrounding floodplains into these estuaries (Walsh et al. 2004).

Drought events can have deleterious impacts on estuarine biota (Copeland 1966). Under drought conditions, estuaries can become “arms” of the sea with high salinity and poor water quality (Scharler and Baird 2005). Drought-induced high salinities result in a loss of freshwater species, declines in estuarine-dependent species and the establishment of marine adventurous species in the lower reaches of estuaries (Vivier and Cyrus 2002; Baptista et al. 2010). Reductions in the delivery of nutrient-enriched freshwater into estuaries can lead to recruitment failure in marine fish. For example, a five-year drought in the San Francisco Bay estuary resulted in reductions in the recruitment success of striped bass due to larval starvation arising from pelagic food

web limitation (Bennett et al. 1995). The production of larval fish exported between estuarine and coastal systems can be significantly reduced during drought (Dolbeth et al. 2008). These alterations to biological productivity can have major impacts on estuarine fisheries. In eastern Australia, for example, the catch rates of estuarine gillnet fisheries decrease by 18-34% during drought (Gillson et al. 2009). In contrast, droughts increase oyster production by elevating oyster growth rates in the Apalachicola estuary on the east coast of North America (Livingston et al. 1997).

Economic impacts of variable flows on estuarine and coastal fisheries

Information on the economic impacts of variable flows on estuarine and coastal fisheries remains elusive. Only a small proportion of the identified articles (10%) alluded to the economic impacts of variable flows on estuarine and coastal fisheries, many without explicitly performing quantitative research (e.g. All 2006; Cardoso et al. 2008). Reduced flows due to droughts can lower the economic performance of commercial fisheries operating in estuarine and coastal systems. Revenue generation from commercial fishing businesses in estuarine and coastal fisheries decreased between 8-36% during periods of drought in eastern Australia (Gillson and Scandol under review). Businesses that operated ocean prawn trawls and estuarine prawn trawls primarily contributed to significant reductions in revenue (Figure 6).

Diversifying harvesting behaviour to target a broad-range of species partially compensated for these reductions in revenue. Commercial fishers, however, would also benefit from augmenting income from enterprises unrelated to fishing during drought. A lack of information on the economic impacts of variable flows on commercial fisheries has hindered the representation of estuarine and coastal systems

in water allocation proposals. Identifying fishing sectors that are economically sensitive to variation in freshwater flow will improve understanding of the freshwater requirements of estuarine and coastal fisheries.

Freshwater requirements of estuarine and coastal fisheries

Conflicts over the allocation of freshwater for human and ecosystem needs are increasingly emerging throughout the world (Poff et al. 2003), particularly in areas of agricultural and ecological importance (Falkenmark 2003). For example, management strategies concerned with allocating freshwater to maintain agricultural production and conserve biodiversity remain highly disputed in the Murray-Darling Basin in eastern Australia (Kingsford et al. In Press). Fortunately, there is increasing recognition that estuarine and coastal systems require a sufficient volume of freshwater to maintain biogeochemical processes (Benson 1981; Sklar and Browder 1998; Powell et al. 2002), but this remains to be quantified in many regions of the world. Knowledge regarding the freshwater requirements of estuarine and coastal systems is far from complete (Gillanders and Kingsford 2002). Information on the freshwater requirements of estuarine and coastal systems is essential to ensure that the interests of commercial fishers are duly represented in decision-making processes associated with the allocation of environmental flows. Recognition that freshwater flow strongly influences fisheries production in estuarine and coastal systems is increasingly emerging in policy, planning and legislation (Montagna et al. 2002).

Methods to determine the freshwater requirements of estuarine and coastal systems have been developed in southern Africa. In the Mtata estuary on the east coast of

southern Africa, for example, mean winter flows $< 4 \text{ m}^3 \text{ s}^{-1}$ favour the colonisation of estuarine biota by promoting natural seasonal flow patterns, establishing a longitudinal salinity gradient and reducing sediment loads (Adams et al. 2002). Simulation models have explored changes to estuarine nursery function under alternative flow scenarios. Annual flows into the Great Brak estuary on the west coast of southern Africa can be halved to $17.35 \times 10^6 \text{ m}^3$ with no discernable effect on fish recruitment but a sharp decline in estuarine immigration resulted thereafter (Quinn et al. 1999). Reduced flows are expected to decrease landings of commercially-important species that currently dominate fisheries harvest. For example, a 44% reduction in freshwater flow from the Thukela River is predicted to decrease commercial landings of slinger (*Chrysoblephus puniceus*) and squaretail kob (*Argyrosomus thorpei*) by 36% and 28% respectively in the Thukela Bank linefishery in KwaZulu-Natal (Lamberth et al. 2009).

A variety of techniques have been presented to manage the delivery of freshwater into estuarine and coastal systems in North America: the optimisation of biological productivity under specified environmental conditions in Texas (Powell et al. 2002); abstraction limits to a percentage of flow at the time of withdrawal in Florida (Flannery et al. 2002); the establishment of salinity gradient ≥ 2 psu to maximise estuarine habitat in California (Kimmerer 2002b); and pulsed freshwater events to maximise oyster production in the Gulf of Mexico (La Peyre et al. 2009).

Less is known about the freshwater requirements of estuarine and coastal systems in Australia. Protecting natural variation in the flow regime is likely to be the most reliable management strategy to maintain fisheries production (Loneragan and Bunn

1999; Robins et al. 2005; Gillson et al. 2009). Seasonal variation in freshwater flow is the most important aspect of the flow regime that influences the production of estuarine and coastal fisheries. For example, summer flows explained the highest proportion (69-80%) of variation in fish and invertebrate landings from the Logan River and Moreton Bay fishery in northern Australia (Loneragan and Bunn 1999). Seasonal pulses of freshwater are particularly important for juvenile fish inhabiting estuarine nursery grounds. For instance, high flows during spring and summer positively influence the recruitment of juvenile barramundi and king threadfin (*Polydactylus macrochir*) in eastern Australia (Staunton-Smith et al. 2004; Halliday et al. 2008).

Ensuring the delivery of freshwater into estuarine and coastal systems is essential to minimise the combined impacts of drought and human water extraction on fish and invertebrates (Whitfield and Bruton 1989; Vivier and Cyrus 2002; Vivier et al. 2010). Identifying the freshwater requirements of estuarine and coastal fisheries is likely to be more difficult in highly regulated catchments, where variability in the flow regime is managed for human requirements. River regulation can dampen hydrological extremes, decouple fisheries–flow relationships and hinder the identification of important aspects of the flow regime for maintaining fisheries production (Gillson et al. 2009). Since many regulated rivers flow across jurisdictional boundaries (Kingsford et al. 1998), the management of freshwater resources over large geographic areas is problematic. Gaining political and managerial consensus in international transboundary rivers has proven difficult (Bernauer 2002). Nevertheless, protecting the goods and services provided by estuarine and coastal ecosystems requires the implementation of integrated water resource management (Jewitt 2002).

An improved understanding of the freshwater requirements of estuarine and coastal fisheries is essential to appreciate the impacts of climate change on fisheries production.

Freshwater flow and fisheries production in a changing climate

Climate change is predicted to have major impacts on fisheries production (Brander 2007), potentially influencing the economies of many developing nations worldwide (Allison et al. 2009). Regional climatic variability is responsible for recent changes in the production of estuarine and coastal fisheries due to alterations in fish distribution and abundance (Roessig et al. 2004; Lehodey et al. 2006; Jennings and Brander 2010). Future changes in climate are expected to spatially redistribute fisheries landings in estuarine and coastal systems (Cheung et al. 2010). Many marine studies predicting the impacts of climate change on fish communities have focused on the effects of warmer temperature (e.g. Perry et al. 2005; Fogarty et al. 2008; Jennings and Brander 2010). In contrast, possible changes to fish communities under alternative freshwater flow scenarios have received relatively little attention.

Increased climatic variability is projected to modify the hydrological cycle with associated changes in rainfall, evaporation, surface runoff, groundwater and freshwater flow (Zestser and Loaiciga 1993; Loaiciga et al. 1996; Milly et al. 2005). Reductions in rainfall and warmer temperatures are expected to decrease freshwater resources in eastern Australia and southern Africa (Kundzewicz et al. 2007). Greater hydrological extremes are predicted to increase the frequency and intensity of flood and drought events in these regions (Meehl et al. 2007). Alterations to freshwater flow

resulting from climate change could be exacerbated by human population growth increasing demand for water resources (Vörösmarty et al. 2000). It is likely that the impacts of future changes in rainfall and freshwater flow on fisheries production will vary between geographic regions. For example, increased monsoonal rainfall is projected to elevate fish production in northern China (Qiu et al. 2010), whereas decreased freshwater flow is projected to reduce penaeid prawn production in eastern Australia (Ives et al. 2009).

Future changes in freshwater flow will modify primary and secondary production by altering the supply of nutrients and organic matter into estuarine and coastal systems (Mallin et al. 1993; Rabalais et al. 1996; Struyf et al. 2004). These changes to primary and secondary production are expected to modify the productivity of commercial fisheries (Kennedy 1990; Lehodey et al. 2006; Jennings and Brander 2010). Estuarine and coastal systems will be mainly impacted by changes to the delivery of nutrient-enriched freshwater through the exacerbation of current stresses such as eutrophication and hypoxia (Vitousek et al. 1997; Cloern 2001; Rabalais et al. 2009). For example, climate predictions indicate a 20% increase in freshwater flow entering the Gulf of Mexico, which is expected to negatively impact coastal biota due to elevated nutrient loads increasing primary production and expanding the oxygen-depleted area (Justić et al. 1996). Eutrophication and hypoxia are arguably the biggest threats to estuarine and coastal fisheries due to the creation of dead zones with limited biological productivity (Diaz and Rosenberg 2008).

Alterations to freshwater flow and rising sea levels are likely to modify habitat availability for fish and invertebrates in estuarine and coastal systems (Kennedy

1990). Increased ocean volume and decreased flows could increase habitat for marine species by expanding saline habitats inland (Cheung et al. 2009). In contrast, upstream saline intrusion could decrease habitat for freshwater species that inhabit lakes and rivers (Ficke et al. 2007). Decreased flows are expected to negatively impact the recruitment of marine fish in estuaries. In eastern Australia, for example, lower flows are expected to reduce the survival of black bream eggs and larvae in estuaries by increasing salinity stratification and hypoxic low-oxygen conditions during the spawning period (Nicholson et al. 2008). Reductions in the extent of riverine plume fronts will decrease offshore concentrations of land-based cues that stimulate larval immigration towards estuarine nursery grounds (Vinagre et al. 2009). Lower flows could modify the phenological activities of estuarine-dependent fish by altering synchrony between the delivery of freshwater flow and recurring life cycle events. Impacts would be most pronounced for anadromous species that require seasonal flows to provide offshore environmental cues for migration towards riverine spawning grounds. For example, the upstream migration of Atlantic salmon (*Salmo salar*) into rivers has been delayed by low flows during hot dry summers in the South West of England (Solomon and Sambrook 2004).

It is unclear exactly how future increases in flood events will impact fisheries production in estuarine and coastal systems. Although climate projections indicate that flooding will increase in frequency and intensity in the future (Meehl et al. 2007), the impacts of more frequent and intense flood events on estuarine and coastal systems have not been predicted in detail. Evidence from recent studies indicates that increased flood occurrence could reduce species abundance and diversity by disrupting food web structure and reducing the availability of high salinity habitat in

estuarine and coastal systems (Whitfield and Harrison 2003; Cardoso et al. 2008; Vinagre et al. 2010). In contrast, the impacts of drought events on estuarine and coastal fisheries have been predicted with greater confidence. More frequent droughts are likely to modify the structure and function of estuarine and coastal systems. In the Tagus estuary on the western coast of Portugal, for example, the increased frequency of droughts is expected to modify food web structure, decrease the availability of nursery habitats and diminish resilience to disturbance events (Vinagre et al. 2010). Changes to ecological processes arising from droughts are likely to negatively impact the productivity of estuarine and coastal fisheries. For instance, future reductions in freshwater flow due to droughts are predicted to decrease commercial landings of penaeid prawns on the east coast of Australia (Ives et al. 2009).

Predicting the impacts of future changes in freshwater flow on estuarine and coastal fisheries is essential to inform long-term policy debate and strategic management issues. It is necessary to identify management strategies that will ensure the sustainability of estuarine and coastal fisheries under circumstances of increased flow variability. Sustainable management of estuarine and coastal fisheries could be achieved by adjusting quotas to relieve fishing pressure on species that are sensitive to variation in freshwater flow associated with climate change. More detailed hydrological projections are required to predict the impacts of future changes in freshwater flow on the productivity of estuarine and coastal fisheries with greater certainty.

Conclusions

Freshwater flow impacts fisheries production by regulating environmental factors that determine habitat availability, trophic interactions and fishers' harvesting behaviour in estuarine and coastal systems. Seasonal and interannual variation in freshwater flow influences the distribution and abundance of fish and invertebrates through changes in growth, survival and recruitment. Flood and drought events have the most pronounced impacts on fisheries production due to rapid changes in physicochemical conditions modifying species richness and diversity. Our current understanding of the impacts of freshwater flow on fisheries production has been limited by an inability to separate the effects of physical aspects of freshwater flow from nutrient delivery aspects. An improved understanding will only emerge as we gain a better appreciation of the effects of variable flows on habitat availability and trophic dynamics. Research emphasis has now shifted to a more holistic approach due to the realisation that freshwater flow influences a myriad of environmental factors that impact the life histories of fish and invertebrates in estuarine and coastal systems.

Estuarine and coastal fisheries are under increasing threat from river regulation modifying natural flow regimes. Protecting natural flow regimes is likely to be the most effective management strategy to maintain the production of estuarine and coastal fisheries. Information on the socio-economic impacts of variable flows on commercial fisheries is required to resolve some of the outstanding problems in determining the freshwater requirements of estuarine and coastal systems.

Understanding the freshwater requirements of estuarine and coastal fisheries will become increasingly important as climate change modifies the hydrological cycle and human population growth increases demand for water resources. Fisheries scientists

and managers must therefore continue to emphasise the important role of freshwater flow in maintaining the production of estuarine and coastal fisheries. Only then will the interests of commercial fishers in estuarine and coastal systems be duly represented in decision-making processes associated with the allocation of environmental flows.

One of the main challenges for scientists seeking to explore relationships between freshwater flow and fisheries production is to understand how variable flows influence resource availability, fishing activity and the economic performance of commercial fisheries in estuarine and coastal systems. Three areas of priority for future research are suggested: investigating connections between seasonal flows and the timing of recurring life cycle events in marine fish; examining relationships between freshwater flow and fishing activity; and developing bio-economic models to predict the effects of variable flows on commercial fisheries under alternative climate scenarios.

Table 1. Examples of relationships between freshwater flow (or rainfall) and landings of fish and invertebrates in estuarine and coastal systems.

Figure 1. A summary of published articles examining the impacts of freshwater flow (or rainfall) on fishery-related research topics in estuarine and coastal systems from 1910 to 2010. A comprehensive search of 5 scientific databases (CSA Illumina, Geobase, ISI Web of Science, Scopus and OvidSP) identified 823 peer-reviewed articles that used the following key-words and search logic: freshwater flow OR rain* AND fish* AND estuar* AND coast*. Synonyms used in the literature search were 'precipitation' OR 'freshwater inflow' OR 'freshwater outflow' OR 'freshwater input' OR 'freshwater output' OR 'freshwater runoff' OR 'freshwater discharge' OR 'river discharge' OR 'river flow' OR 'river inflow' OR 'river outflow' OR 'river input' OR 'river output' OR 'river runoff' OR 'riverine flow' OR 'riverine inflow' OR 'riverine outflow' OR 'riverine input' OR 'riverine output' OR 'riverine runoff' OR 'riverine discharge' OR 'streamflow' OR 'stream flow' OR 'stream discharge' OR 'stream inflow' OR 'stream outflow' OR 'stream input' OR 'stream output' OR 'stream runoff' OR 'stream discharge' OR 'fluvial flow' OR 'fluvial flow' OR 'fluvial discharge' OR 'fluvial inflow' OR 'fluvial outflow' OR 'fluvial input' OR 'fluvial output' OR 'fluvial runoff' OR 'fluvial discharge'.

Figure 2. A global comparison of the coefficient of variation for annual freshwater flow in river catchments greater than 1000 km². The number of river systems examined in each location is shown in parentheses above each bar. (Modified from Finlayson and McMahon 1988).

Figure 3. Relationships between \log_{10} catch per unit effort for dusky flathead and minimum spring flow in the Clarence (a), Hunter (b) and Hawkesbury (c) River estuaries of eastern Australia. * $P < 0.05$; ** $P < 0.01$; $n = 10$. Minimum flow indicates the lowest spring flows. (Modified from Gillson et al. 2009).

Figure 4. A conceptual model illustrating the controlling influence of freshwater flow on the production of estuarine and coastal fisheries. Note that freshwater flow influences fisheries production by regulating habitat availability (white arrows), trophic interactions (grey arrows) and fishers' harvesting behaviour (black arrows) in estuarine and coastal systems.

Figure 5. Difference index of landings per guild (kg of each guild per month) between flood and drought events in the estuarine and coastal fisheries associated with the Clarence, Hunter and Hawkesbury Rivers of eastern Australia. Results based on fourth-root transformed data. Estuarine use guilds consisted of Amphidromous (AM); Catadromous (CA); Estuarine Migrant (EM); Estuarine Resident (ER); Marine estuarine Dependent (MD); Marine estuarine-Opportunist (MO); and Marine Straggler (MS). (Modified from Gillson et al. under review).

Figure 6. Mean revenue per month (AU\$ millions) from the three most financially productive fishing methods during non-drought (white bars) and drought (black bars) conditions in the estuarine and coastal fisheries associated with the Clarence, Hunter and Hawkesbury Rivers of eastern Australia. Fishing method abbreviations are Estuarine Prawn Trawl (EPT), Gillnetting (GI), Hauling Net (HN) and Ocean Prawn Trawl (OPT). (Modified from Gillson and Scandol under review).

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Acknowledgements

Thanks to the University of New South Wales Evolution and Ecology Research Centre for providing funding for this project. I am grateful to Iain Suthers and James Scandol for providing constructive comments on the development of this manuscript.