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Review

Freshwater-flow requirements of estuarine fisheries in tropical Australia: a review of the state of knowledge and application of a suggested approach

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Abstract. The freshwater-flow requirements of estuarine fisheries in tropical areas are reviewed, with reference to species important to fisheries in northern Australia. Fisheries production, in terms of catch, is often elevated during, or as a consequence of, years with higher river flow, but the causality of these relationships often remains unproven. Scientific information on the freshwater-flow requirements important to fisheries production is increasingly being sought during the planning, allocation and management of water resources within Australia and in other countries around the world. Frequently, such advice is based on the analysis of catch and freshwater flow (or rainfall), or on life-history information. Clarifying fisheries-specific goals of water management would assist in prioritising research into the freshwater-flow requirements of estuarine fisheries. A framework that integrates life-history information and correlative analyses is suggested to assist in understanding the freshwater-flow requirements of estuarine fisheries. The framework is also useful in identifying knowledge gaps and pertinent research questions. The approach is illustrated through its application to identifying key freshwater-flow events likely to be important for fisheries production in a dry tropical estuary in Queensland, Australia.

Extra keywords: banana prawns, barramundi, conceptual framework, environmental flows, mud crabs.

Introduction

In estuaries and near-shore waters of tropical Australia, there are commercial fisheries for penaeid prawns (*Penaeus merguiensis*, *P. indicus*, *P. esculentus*, *P. semisulcatus*, *Metapenaeus ensis*, *M. endeavouri*), finfish (*Lates calcarifer*, *Polydactylus macrochir*, *Eleutheronema tetradactylum*, *Lutjanus johnii*, *Protonibea diacanthus*, *Pomadasys kaakan*, *P. argenteus*, *Scomberomorous semifasciatus*, *Mugil* sp., *Liza vaigiensis*, *L. argentea*, *Scomberoides lysan*, *S. commersonianus*), sharks (*Carcharhinus tilstoni*, *C. sorrah*) and crabs (*Scylla serrata*), with a combined annual value of about AU$220 million. Some species are also important recreationally (e.g. barramundi (*L. calcarifer*) and mud crabs (*S. serrata*)) and to indigenous communities. Many of the above species are dependent on estuarine ecosystems during their lifecycle and are influenced by fresh water flowing into the estuary. In tropical Australia, freshwater inflow to estuaries is influenced by the seasonal summer monsoon trough, with increased flow during late spring (October, November) and summer (December–February) and decreased flow during winter (June–August) and early spring (September). The timing, duration and magnitude of fresh water flowing to estuaries may change as a consequence of the development of water resources, and these changes impact on estuarine species (Drinkwater and Frank 1994; Gillanders and Kingsford 2002).

Water resources are highly developed in some areas of tropical Australia (e.g. Queensland east coast) and are being planned for 'development' in others (e.g. Gulf of Carpentaria and Northern Territory). Within Australia, and worldwide, there is increasing recognition of the need to allocate water for the environment as part of the sustainable use of water resources (Davis and Hirji 2003*a*, 2003*b*, 2003*c*; Dyson *et al*. 2003). Water for the environment is referred to as environmental-flow allocations (Tharme 2003), freshwater-inflow needs (Powell *et al*. 2002) or freshwater-inflow requirements (Adams *et al*. 2002). In Australia, environmental flows are allocated to maintain the health

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and viability of water-dependent ecosystems (including estuaries) in catchments where water resources are managed. Estuarine fisheries species and their productivity (i.e. catch) have been proposed as tangible indicators of estuarine ecosystem health linked to environmental-flow allocations. This is because fisheries species have economic and social value and are often the only species for which sufficient life-history information and/or long-term abundance data (in the form of catch) are available. Alber (2002) suggested that linking freshwater flows to important fishery species is a relatively simple relationship that can be easily understood by a range of stakeholders, even if the underlying mechanisms are not certain.

Drinkwater and Frank (1994) reviewed the general effects that fresh water may have on fish and invertebrates in coastal and marine waters, concluding that the number and geographic extent of examples strongly supports a link between freshwater flow and production of certain estuarine and marine fish and shellfish. Proposed mechanisms for the connection between estuarine fishery species and freshwater flow include: (*i*) trophic linkages via changes to primary or secondary production that result from the addition of nutrients; (*ii*) changes in distribution as a consequence of altered (expanded, reduced or connected) habitats; and (*iii*) changes in population dynamics such as recruitment, growth, survival and abundance (Copeland 1966; Aleem 1972; Peters 1982; Drinkwater 1986; Drinkwater and Frank 1994; Loneragan and Bunn 1999; Gillanders and Kingsford 2002). Most effects on estuarine fishery species are one or more steps removed from the direct changes in physical parameters (e.g. water velocity, salinity, water temperature, turbidity) that result from fresh water flowing into estuaries (Drinkwater 1986; Hart and Finelli 1999; Alber 2002; Kimmerer 2002*a*).

Review of the relationships between freshwater flow and fisheries catch of tropical species

Frequently, knowledge of the freshwater-flow requirements of fisheries is based on the analysis of catch (= landings) and freshwater-flow data. Relationships between catch of estuarine or near-coastal fishery species and freshwater flow (or rainfall as a proxy of freshwater flow) have been reported for more than 20 tropical (or subtropical) species (Table 1). Studies in subtropical areas were included in our review because of the extended distribution of some species into subtropical areas, as well as the limited number of studies occurring completely within the tropics. Relationships between freshwater flow and commercial catch have also been investigated for temperate species (see Sutcliffe 1973; Sutcliffe *et al.* 1977; Drinkwater and Myers 1987; Ardisson and Bourget 1997; Skreslet 1997; Perry *et al.* 2000; Lloret *et al.* 2001; Salen-Picard *et al.* 2002). Temperate studies include a greater number of finfish and mollusc species, whereas tropical (and subtropical) studies include a greater number of crustacean species (i.e. peneaid prawns = shrimp).

Correlation or regression analysis to identify environmental variables that contribute to variation in fisheries catch can be criticised because of: (*i*) the confounding effects of stock size and fishing pressure (Walters and Collie 1988); (*ii*) the likely non-linearity of linking mechanisms (Baumann 1998) and the probability of multiple mechanisms; (*iii*) the possibility of type I errors (i.e. false significant correlations, Potter *et al.* 2001); (*iv*) the lack of ability to prove causality (Quiñones and Montes 2001); and (*v*) their uncertain predictive capability as a consequence of long-term climatic variation or human-induced changes (e.g. habitat loss, pollution). Although an experimental approach is needed to determine causality, manipulative experiments of freshwater flow are rarely practical at the scale of whole estuaries and it is difficult to obtain appropriate controls for 'before–after control–impact' experiments that utilise ongoing human manipulation of freshwater flows (i.e. water regulation). Therefore, in many instances, observational studies are used to derive insights into the factors driving the distribution and abundance of fisheries species at a whole-of-estuary scale, with correlation or regression analysis of catch data and environmental variables (e.g. rainfall or freshwater flow) being used to identify which factors are likely to be important (Tyler 1992).

Most studies of tropical fishery species report positive relationships between catch and increased freshwater flow (Table 1). The variables that explain the greatest amount of variation in catch are not consistent and the patterns differ for the same species in different areas and for different species in the same area. However, as discussed below, the proposed mechanisms underlying the observed relationships are relatively consistent within the species groups.

Penaeid prawns

Peneaid prawns (= shrimp) are targeted by major commercial fisheries in tropical and subtropical Australia, as well as in many other parts of the world. Penaeid prawns are short-lived (i.e. one to two years), opportunistic omnivores (Chong and Sasekumar 1981). Many species of penaeid prawn are dependent on estuarine habitats for part of their life cycle, but have different preferences of habitat type, degree of emigration and tolerance of low salinity. Freshwater flow (or rainfall) has been related to catch for ten species of penaeid prawn (Table 1). Most correlations between freshwater flow (or rainfall) and prawn catch have been reported for those species with the greatest tolerance or exploitation of brackish-water habitats. In general, significant positive relationships occur between annual catch and total freshwater flow (or rainfall) in the same or previous year (Gunter and Hildebrand 1954; Ruello 1973; Glaister 1978; Vance *et al.* 1985; Gammelsrod 1992; Galindo-Bect *et al.* 2000). Significant within-year correlations between catch and monthly or

Table 1. Summary of studies investigating relationships between fisheries catch (= landings) and freshwater flow (or rainfall) for species found in tropical and subtropical areas

Species	Location	Direction of relationship	Reference
Penaeus merguiensis, banana prawn	Australia, Gulf of Carpentaria	Positive	Vance *et al*. 1985, 1998; Staples and Vance 1986
	Papua New Guinea, Gulf of Papua	Negative	Evans *et al*. 1997
Penaeus indicus, red-legged banana prawn	Mozambique	Positive	da Silva 1985; Gammelsrod 1992
Metapenaeus macleayi, school prawn	Australia, northern New South Wales	Positive	Ruello 1973; Glaister 1978
Penaeus plejebus, king prawn	Australia, southeast Queensland	Positive	Loneragan and Bunn 1999
Penaeus esculentus, tiger prawn	Australia, southeast Queensland	Positive	Loneragan and Bunn 1999
Metapenaeus bennettae, greasy prawn	Australia, southeast Queensland	Positive	Loneragan and Bunn 1999
Penaeus setiferus, white shrimp	USA, Texas	Positive	Gunter and Hildebrand 1954; Powell *et al*. 2002
Penaeus aztecus, brown shrimp	USA, Texas	Positive	Powell *et al*. 2002
Penaeus duorarum, pink shrimp	USA, Gulf of Mexico	Positive	Browder 1985; Browder *et al*. 2002
Litopenaeus stylirostris	Mexico, Gulf of California	Positive	Galindo-Bect *et al*. 2000
Eleginops maclovinus, Róbalo	Chile, central-south coast	Negative	Quiñones and Montes 2001
Sciaenops ocellatus, red drum	USA, Texas	Positive & negative	Funicelli 1984; Powell *et al*. 2002
Pogonias cromis, black drum	USA, Texas, Guadalupe Estuary	Positive & negative	Powell *et al*. 2002
Cynoscion nebulous, spotted seatrout	USA, Texas	Positive & negative	Funicelli 1984; Powell *et al*. 2002
Mugil sp., mullet	Australia, southeast Queensland	Positive	Loneragan and Bunn 1999
Sillago so. whiting	Australia, southeast Queensland	nsc	Loneragan and Bunn 1999
Platycephalus sp., flathead	Australia, southeast Queensland	Positive	Loneragan and Bunn 1999
Callinectes sapidus, blue crab	USA, Florida and Texas	Positive & negative	Meeter *et al*. 1979; Funicelli 1984; Powell *et al*. 2002
Portunus pelagicus, blue swimmer crab	Australia, southeast Queensland	nsc	Loneragan and Bunn 1999
Scylla serrata, mud crab	Australia, southeast Queensland	Positive	Loneragan and Bunn 1999
Crassostrea virginica, eastern oyster	USA, Florida and Gulf of Mexico	Positive & negative	Meeter *et al*. 1979; Funicelli 1984; Wilbur 1992; Powell *et al*. 2002
Octopus vulgaris, common octopus	Spain, Gulf of Cadiz	Negative	Sobrino *et al*. 2002
Sepia officinalis, cuttlefish	Spain, Gulf of Cadiz	nsc	Sobrino *et al*. 2002

nsc = No significant correlations.

seasonal freshwater flow (or rainfall) have also been reported (Glaister 1978; Browder 1985; da Silva 1985; Vance *et al*. 1985, 1998; Gammelsrod 1992). The relationship between catch and freshwater flow (or rainfall) is not always consistent between areas, even for the same species. For example, negative correlations between prawn catch and rainfall have been reported in the Gulf of Papua, Papua New Guinea (Evans *et al*. 1997), whereas significant positive correlations between prawn catch and rainfall have been reported for some areas of the Gulf of Carpentaria, Australia (Vance *et al*. 1985). This example demonstrates that the relationship between prawn catch and freshwater flow should be assessed for individual estuaries to account for hydrological and biological differences between catchments (Vance *et al*. 1998).

The relationships between prawn catch and freshwater flow (or rainfall) are potentially confounded by other factors such as fishing effort and spawning stock size (Browder 1985; da Silva 1985). Their degree of influence depends on the level of exploitation of the population by the fishery (Vance *et al*. 1985), although most of the correlative studies for prawns do not account for these factors.

Suggested causal mechanisms for the observed relationships between the catch of peneaid prawns and increased freshwater flow (or rainfall) include: (*i*) enhanced emigration of prawns to areas accessible to the fishery, leading to increased catchability (Ruello 1973; Glaister 1978; da Silva 1985; Gammelsrod 1992; Evans *et al*. 1997; Vance *et al*. 1998); and (*ii*) enhanced growth and survival of various life stages, leading to increased abundance or biomass (Ruello 1973; Evans *et al*. 1997), through enhanced recruitment from enlarged nursery areas (Browder 1985; Gammelsrod 1992; Galindo-Bect *et al*. 2000), and/or enhanced food availability from increased primary and secondary productivity (Loneragan and Bunn 1999).

Although the conclusions of most correlative studies are speculative, other evidence supports the likelihood of these mechanisms. For example, emigration rates of juvenile banana prawns from estuaries to near-shore areas is strongly linked to rainfall events (Staples and Vance 1986; Vance *et al*. 1998) and emigration rates are significantly correlated with commercial catches (Staples and Vance 1986, 1987; Vance *et al*. 1998). Experimental studies demonstrate that the growth of penaeid prawns is influenced strongly by temperature and salinity, and that there are temperature-by-salinity optima for each species (Staples and Heales 1991; Haywood and Staples 1993; Vinod *et al*. 1996). The possibility of a salinity-by-temperature optimum that influences the growth and survival of prawn life stages potentially explains the parabolic relationship between prawn catch and rainfall in the Gulf of Papua suggested by Evans *et al*. (1997), where high rainfall (= high freshwater flow and low salinity) reduces the immigration and survival of larvae and post-larvae, intermediate rainfall (= intermediate freshwater flow and intermediate salinity) stimulates emigration to offshore waters, and low rainfall (= low freshwater flow and high salinity) reduces emigration to offshore waters. Enlarged nursery areas may occur as a result of freshwater flows providing favourable salinity ranges over the greatest amount of suitable and accessible areas of nursery habitat during critical life stages of pink shrimp (*Penaeus duorarum*) (Browder *et al*. 2002).

Finfish fisheries

Relationships between commercial catch and freshwater flow have been published for seven tropical (or subtropical) finfish species in estuarine or coastal areas of the USA, Mexico, South America and Australia (Table 1). Although not a quantitative study, Aleem (1972) described a dramatic decrease in the catch of *Sardinella* sp. in the Mediterranean Sea as a consequence of damming the Nile River and eliminating floods. In subtropical Australia, significant positive correlations between catch and freshwater flow were found for mullet (*Mugil* spp.) and flathead (*Platycephalus* spp.) (Loneragan and Bunn 1999). In central–south Chile, significant negative correlations between catch and freshwater flow were reported for róbalo (*Eleginops maclovinus*) (Quiñones and Montes 2001); and in the USA, catches of red drum (*Scianeops ocellatus*), black drum (*Pogonias cromis*) and spotted seatrout (*Cynoscion nebulous*) have been both negatively and positively related to freshwater flow aggregated into two-monthly totals (Powell *et al*. 2002).

Suggested causal mechanisms for the observed relationships between finfish catch and freshwater flow include: (*i*) changes to catchability (Loneragan and Bunn 1999); (*ii*) changes to cohort or year-class strength during the first year of life (Quiñones and Montes 2001); and (*iii*) changes to food availability via productivity changes resulting from flow-borne nutrients (Aleem 1972; Salen-Picard *et al*. 2002). Effects on catchability are suggested where correlations between catch and freshwater flow occur within a relatively short period, suggesting an immediate response (e.g. within the same year for annual correlations). In southern Queensland, increases in catchability are proposed to be the consequence of restricting the distribution or stimulating the movement of flathead species (Loneragan and Bunn 1999). Anecdotal reports from commercial fishers in tropical Australian estuaries suggest that barramundi may also be stimulated to move by freshwater flows, both from upstream habitats as well as moving around within estuarine habitats, thus increasing their catchability in passive fishing gear (i.e. set gillnets). However, the movement of barramundi from upstream habitats requires that individuals be abundant in such habitats.

Effects on year-class strength are suggested where significant correlations are between catch and freshwater flow, lagged by the period that it takes individuals of the species to 'recruit' to the fishery (suggesting a lagged response). The proposed mechanisms include: (*i*) advection (negative effect) or retention (positive effect) of eggs and larvae in nursery areas; (*ii*) increased predation (negative effect) on young-of-the-year; (*iii*) expansion of suitable reproductive and nursery habitats; and (*iv*) improved food availability for larvae and juveniles (Quiñones and Montes 2001; Salen-Picard *et al*. 2002). Few studies have investigated the causal mechanisms in detail, although Kimmerer *et al*. (2001) reassessed the effects of freshwater flow on the early life history of striped bass (*Morone saxatilis*) in the San Francisco Estuary. They found that strong relationships existed between freshwater flow and survival from eggs to young-of-the-year, but that recruitment of three-year-olds was not related to freshwater flow during the early life stages. North and Houde (2003) studied the effects of freshwater flow on the early life history of striped bass and white perch (*M. americana*) in upper Chesapeake Bay (a temperate estuary). They reported that freshwater-flow conditions were strongly related to physical conditions, prey concentrations and larval-fish distributions associated with the estuarine-turbidity-maxima nursery area.

These three effects (i.e. catchability, abundance and productivity) are not mutually exclusive. It is likely that each of these mechanisms contribute to the fluctuations in catches of finfish species that are significantly correlated to freshwater inflow to estuaries.

Other species – crabs, oysters and octopus

Crabs are common in tropical estuaries throughout the world and are the target species of many fisheries. Relationships between commercial catch and freshwater flow have been investigated for the mud crab, which is the main commercial crab species in tropical Australia, as well as for blue swimmer crabs (*Portunus pelagicus*) and blue crabs (*Callinectes sapidus*) (Table 1). Annual catches of mud crab were positively correlated with summer freshwater flow; possible causal mechanisms include: (*i*) an increase in catchability resulting from freshwater flow stimulating downstream movement; and (*ii*) an increase in the survival of juveniles through reduced cannibalism and competition for burrows as a consequence of the emigration of adult crabs (Loneragan and Bunn 1999). Blue swimmer crabs and blue crabs are conspecifics, occurring in estuaries of the southern and northern hemispheres respectively. No significant correlations between catch and seasonal freshwater flow were reported for blue swimmer crabs (Loneragan and Bunn 1999), but seasonal freshwater flow explained a significant proportion of the variation in the annual catch of blue crabs in numerous estuaries of the USA (Meeter *et al*. 1979; Funicelli 1984; Powell *et al*. 2002).

Oyster harvest has been negatively correlated to freshwater flow in the same year (Meeter *et al*. 1979; Wilbur 1992) and positively correlated to freshwater flow in previous years (Wilbur 1992). Significant negative and positive relationships between oyster harvest and seasonal freshwater flow were also reported by Powell *et al*. (2002). Freshwater flow is suggested to negatively affect growth (Meeter *et al*. 1979), mortality and spawning (Wilbur 1992). Livingston *et al*. (2000) suggested that freshwater flow affects oyster production through two mechanisms: (*i*) predation and disease related to changes in salinity; and (*ii*) growth effects related to changes in the trophic productivity of the estuary.

Significant negative correlations between catch and freshwater flow were reported for octopus (*Octopus vulgaris*) in the Gulf of Cadiz, Spain, but not for cuttlefish (*Sepia officinalis*, Sobrino *et al*. 2002). Fluctuations in octopus catch were suggested to be a consequence of environmentally driven variation in recruitment and that freshwater flow (= river flow) changed environmental conditions and stimulated the movement of octopus from their dens.

Relevance of correlative studies to the freshwater-flow requirements of estuarine fisheries in tropical areas

The additional studies reported in the literature since the review of Drinkwater and Frank (1994) reinforce the conclusion that the catch of some estuarine and marine finfish and shellfish is strongly linked to freshwater flow, being equally applicable in tropical, subtropical and temperate areas. The correlative studies demonstrate that seasonality is often as important as the volume of the flow (Loneragan and Bunn 1999), and that freshwater-flow requirements of fished species need to be assessed on a species-by-estuary basis. Relationships between catch of estuarine species and freshwater flow have been included in models designed to optimise freshwater inflows over specified physical, chemical and biological constraints in Texas, USA (Bao and Mays 1994; Powell *et al*. 2002). However, this method depends on large quantities of catch data, which are unlikely to be available for most estuaries.

Drinkwater and Frank (1994) recommended that more quantitative research was needed into the relationship between freshwater flows for fish and ecosystems, including multidisciplinary studies and integrated physical–biological models. This would lead to greater knowledge of the mechanisms underlying the relationships between catch and freshwater flows and would help to determine which aspects of the flow regime were important. Kimmerer (2002*a*, 2002*b*) and Browder *et al*. (2002) reiterated the need to understand the causal mechanisms in the relationship between freshwater flow and (the biology of) the species of interest. Conceptual models of the role of freshwater flow in estuarine ecosystems, and hypotheses developed from them, need to be explicitly considered in order to direct multidisciplinary studies and to provide the conceptual structure for integrated biophysical models.

An integrated approach

Advice on the freshwater-flow requirements of fisheries is being sought currently, and the legal and political ramifications of the water allocation process prohibit delaying these allocations until greater understanding of ecosystem functioning is achieved. Therefore, a more structured and transparent method is needed to identify the freshwater-flow requirements for fisheries using the available information. We developed a framework to identify aspects of the freshwater-flow regime that are potentially important for estuarine shellfish and finfish species (Fig. 1). Conceptual models (with hypotheses) of key biological processes of estuarine fisheries resources that are flow dependent were developed and refined using a combination of life-history information and analysis of catch and freshwater-flow data. The results can be used to identify key flow events that are ecologically important (*sensu* Gippel 2002) and that contribute to estuarine ecosystem health. In addition, our approach identifies priority areas of research in order to 'test' or gather more evidence in support of any particular hypothesis.

Assessment of life history

Assessing life-history information aims to identify the biological processes for estuarine or near-coastal fishery species that are affected by freshwater flows and also highlights gaps in the knowledge. Our assessment criteria were based on categories of freshwater-flow effects identified by Drinkwater and Frank (1994), i.e. spawning success, advection of eggs and larvae, migration, competition and distribution, general productivity and food supply and water quality. However, migration and distribution are considered together because of the similarity in their relationship with freshwater flow, and water quality is not included as a specific category, but rather effects on water quality are integrated into the other categories.

Assessing the role of freshwater flows on spawning success includes impacts on the survival of eggs and larvae. Issues considered may include the timing of spawning in relation to freshwater-flow events, triggers for the act of spawning, whether the quality of spawning habitat (including water-quality parameters) is reliant on, or affected by, freshwater flows (e.g. intermittently closed estuaries), and if so, what factors are affected. The role of freshwater flow on the advection of eggs and larvae should identify whether eggs and/or larvae are influenced by currents or chemical

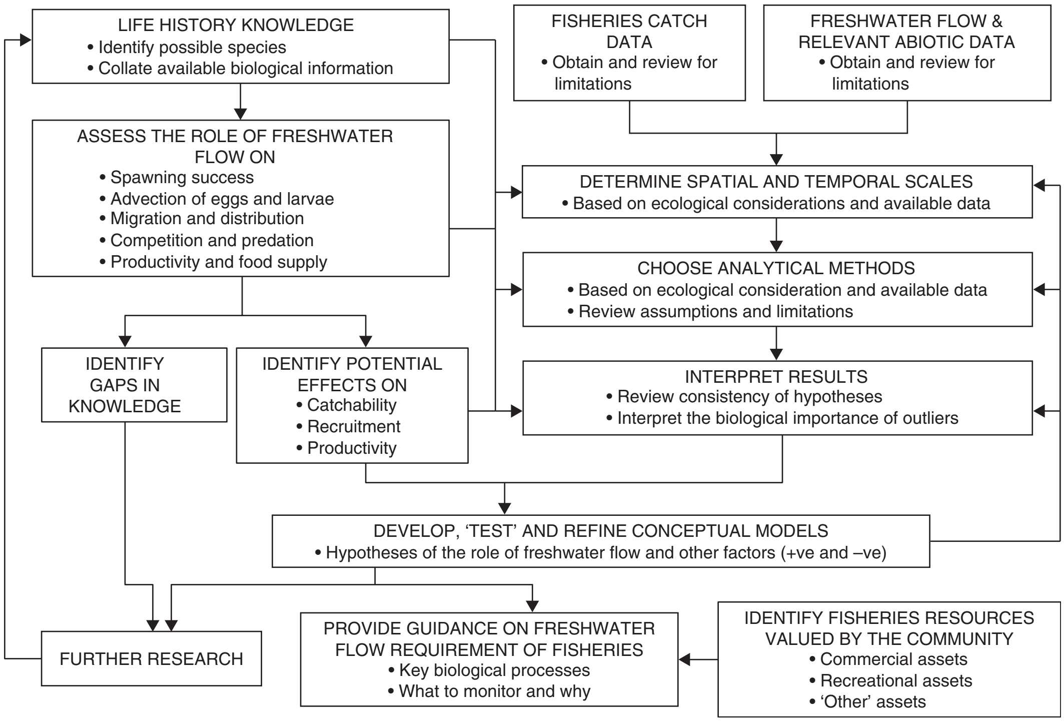

Fig. 1. Generalised framework (logical approach) to identifying aspects of the freshwater-flow regime that are potentially important to estuarine fisheries production.

cues resulting from freshwater-flow events. Issues regarding the effects of freshwater flow on migration and distribution include how flow affects the distribution of each life-history stage, causes of the change in distribution (i.e. as a consequence of habitat access, food availability, salinity gradients or turbidity), effects on nursery habitats (e.g. connections, longevity and water quality) and triggers for the migration of adults (i.e. spawning migration) or juveniles (including the relevance of other factors in stimulating migration, e.g. daylength, water temperature and lunar phase). Effects on the catchability of a species resulting from migration or changes in distribution patterns should be identified. Assessing the role of freshwater flows on competition includes effects on predation that may result from increased turbidity or changed distribution of predators. The trophic level of the species can be assessed to determine how changes in primary productivity occurring as a consequence of freshwater flows could translate to changes in the productivity of the species, including changes in growth rates resulting in increased biomass per recruit.

Proposed mechanisms of the role of freshwater flow can be then summarised into effects on: (*i*) catchability; (*ii*) recruitment (i.e. survival during early stages of life, which translates to the 'strength' or size of a cohort); and (*iii*) productivity, such as increased growth rates. Examination of the proposed mechanisms allow the *a priori* identification of freshwater-flow variables to be used in the analysis of fisheries catch data, as recommended by Tyler (1992).

Analysis of catch data

We suggest that the analysis of catch and freshwater-flow data can be made more robust by critically selecting data for analysis, choosing analytical methods appropriate to the data limitations and critically interpreting the results (Fig. 1).

Fisheries catch data is influenced by numerous factors (e.g. stock-recruitment relationships, levels of fishing effort, habitat changes, pollution impacts and other density-dependent processes such as competition and predation). The impacts of such factors on the catch should be considered and, where possible, species for which these impacts are minimal, constant or measurable, be selected for analysis. The degree to which a species migrates should also be considered because correlative analyses between freshwater flow and catch may not be appropriate for species that undertake extensive spawning migrations (e.g. mullet *Mugil cephalus*) or that have broad-scale dispersal mechanisms of eggs or larvae (e.g. eastern king prawns *Penaeus plejebus*). Fresh water flowing to estuaries is often based on gauged data from a station located upstream of the estuary. Freshwater-flow data may need to be revised to include water extractions or additional freshwater flows from ungauged streams or tributaries occurring downstream of the gauging station. The spatial

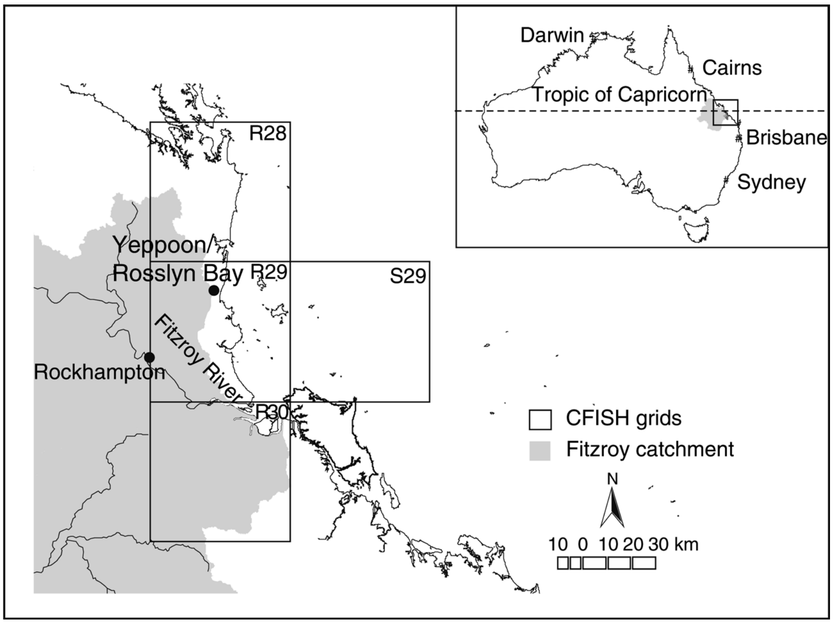

Fig. 2. Locality map of the Fitzroy River estuary, showing depots of the Queensland Fish Board (Rockhampton, Rosslyn Bay and Yeppoon) and CFISH grids (R28, R29, R30, S29), which represent the spatial aggregation of the fisheries catch data for 1945 to 1980 and 1988 to 2002 respectively. A tidal barrage is located on the Fitzroy River at Rockhampton.

(and temporal) scales at which fisheries and freshwater-flow data are aggregated should appropriately represent the area of influence of freshwater flow on the fished species. Consideration should be given to the appropriate analytical method and whether autocorrelation is a feature of the data (Pyper and Peterman 1998). Results from the analysis should be reviewed for consistency with the theoretical mechanisms proposed before the analysis, and we suggest that further consideration be given to interpreting anomalous observations (i.e. 'outliers' where the relationship between catch and freshwater flow does not conform to the analytical model). Such observations may provide insights into other factors (positively or negatively) influencing fisheries catch.

Results from the analysis of catch and freshwater-flow data can be used to identify which of the proposed mechanisms are supported by the available evidence and therefore (from the available evidence of life-history assessment and analysis of data) identify the biological processes of estuarine fishery species that are likely to require freshwater flows.

A case study in a tropical Australian estuary

We investigated the role of freshwater flows in estuarine fisheries of a dry topical region on the Queensland east coast. We applied the integrated assessment of life-history information and analysis of catch and freshwater flow to develop conceptual models with hypotheses of the effect of freshwater flow on populations of fishery species. Our approach and preliminary results are presented for three species, banana prawns, barramundi and mud crabs, that are important estuarine species throughout tropical Australia and for which freshwater-flow requirements are of interest to Australian water and fisheries managers. In addition, these species occur, or have conspecifics, in tropical estuaries in other parts of the world.

The Fitzroy River estuary

The Fitzroy River has a large, mangrove-fringed estuary that straddles the Tropic of Capricorn, and receives freshwater flow from the largest catchment (142 537 km^2) on the east coast of Australia (Fig. 2). A tidal barrage was constructed in 1970, about 50 km upstream of the river mouth. The substratum is predominately mud and there is a complex of islands and channels in the delta. Some islands are covered in mangroves, others have mangrove fringes with intertidal saltmarshes and there are also extensive saltpans (Long and McKinnon 2002).

The Fitzroy catchment is outside (i.e. south) the summer monsoon trough that occurs seasonally over tropical Australia. High variation in annual freshwater flow and rainfall are characteristic of the region. Mean annual (i.e. September to August) freshwater flow is 5.2 million ML (164.8 $m^3 s^{-1}$), with recorded minimum and maximum annual flows of 0.08 million ML (2.5 $m^3 s^{-1}$) and 37.3 million ML (1182.7 $m^3 s^{-1}$) respectively. Patterns of freshwater flow in the Fitzroy River are typical of estuaries in subtropical and tropical Australia, being dominated by summer floods and winter droughts, but varying seasonally as a consequence of rainfall patterns. In general, seasonal increases in freshwater flow occur between November and May, with the largest average monthly flows occurring in February. Between June and October, freshwater flow can drop to almost zero. Water resources in the Fitzroy River are highly regulated, via 19 dams (including weirs) and one tidal barrage. However, this infrastructure is unable to withhold seasonal episodic floods associated with low-pressure systems.

Commercial fisheries of the Fitzroy region are typical of tropical estuaries and inshore areas of northern Australia. There are trawl fisheries for penaeid prawns, net fisheries for estuarine finfish and trap fisheries for crabs. The trawl fishery for prawns has two components: a within-estuary (river) beam-trawl fishery and an offshore (and coastal foreshore) otter-trawl fishery. This arrangement is typical of estuaries and adjacent areas of the Queensland east coast, but not of the Gulf of Carpentaria or Northern Territory (i.e. Northern Prawn Fishery), where there is only an offshore trawl fishery.

Life-history assessment

Banana prawns

Numerous studies have suggested that freshwater flow influences banana prawn populations, although whether this holds for the central Queensland area is unknown. Based on the published literature, we identified the following theoretical mechanisms of the effects of freshwater flow on: (*i*) recruitment, by (*a*) washing away eggs and larvae thereby reducing larval immigration to the estuary (negative effect), or (*b*) stimulating the larvae to enter the estuary in response to chemical cues; (*ii*) catchability, by stimulating the downstream movement of juvenile and subadult banana prawns; and (*iii*) productivity, through increased food availability resulting from enhanced biological productivity of the estuary, resulting in improved growth and survival of post-larvae, juveniles and adolescents.

Barramundi

No studies have published correlations between the catch of barramundi and freshwater flow. However, numerous aspects of barramundi life history suggest that populations are likely to be highly responsive to freshwater flows. Dunstan (1959) and Williams (2002) proposed that the catch of barramundi is closely associated with freshwater flows and/or rainfall, through influencing adult spawning success, juvenile recruitment and catchability. Barramundi can move large distances between estuaries, but most individuals remain within a specified region (Davis 1986; Salini and Shaklee 1988; Keenan 1994). Tag–recapture information indicated that this is also true of barramundi in the Fitzroy River region (Australian National Sportfishing Association Queensland Inc., Infofish Services, Rockhampton, unpublished data), suggesting that changes in local freshwater-flow conditions may be reflected in the local catches. In tropical Australia, commercial barramundi fisheries are restricted by fisheries regulations to estuarine and marine waters, despite barramundi using freshwater habitats as juveniles (i.e. it is a diadromous species).

Detailed accounts of barramundi life history in Australian estuaries can be found in Dunstan (1959), Davis (1985), Russell and Garrett (1985) and Griffin (1987). Assessment of life-history information identified that freshwater flow could influence the life history of barramundi in the following ways: (*i*) on catchability in the estuary, by (*a*) stimulating the downstream migration of mature barramundi (in preparation for estuarine spawning), (*b*) enabling downstream migration of mature individuals through the connection of habitats intermittently linked to the river or estuary and (*c*) changing the distribution of individuals within the estuary (by stimulating within-estuary movement), thereby increasing the chance of being caught in the set gill-net fishery; (*ii*) on recruitment, by (*a*) transporting eggs and larvae away from the estuary (negative effect), (*b*) creating chemical signals for larvae to enter the estuary and locate nursery habitats (positive effect), (*c*) enabling post-larvae and small juveniles to move into supralittoral nursery habitats and (*d*) enabling large juveniles to migrate into freshwater habitats intermittently linked to the estuary; and (*iii*) on productivity, by increasing food availability as a consequence of enhanced biological productivity of the estuary, thereby improving the growth and survival of post-larvae, juveniles, adolescents and adults.

Mud crabs

We found conflicting evidence in the available life-history information about the influence of freshwater flows on mud crabs. The life cycle of the mud crab involves several stages and uses both marine offshore areas and estuaries (Arriola 1940). In tropical Australia, mated ovigerous female mud crabs migrate to offshore waters, but the timing of the migration (i.e. before the monsoon season) suggests that the spawning migration is not triggered by low salinities in estuaries (Hill 1994). Early life-history stages of mud crabs (i.e. eggs, zoeal and megalopal larval stages) require high salinities (i.e. >20 on the practical salinity scale of 1978, UNESCO 1981), with considerable mortality occurring at salinities below 20 (Hill 1974; Quinn and Kojis 1987). Recruitment success of mud crabs in Madagascar was estimated to be seasonal and inversely related to rainfall (Le Reste *et al*. 1976). However, flooding associated with cyclones had little measurable effect on the recruitment of the megalopa larvae of mud crabs in the St Lucia estuary, South Africa (Forbes and Hay 1988). Under experimental conditions, adult mud crabs showed varying levels of mortality after exposure to different salinities, but did not show an ability to discriminate between salinities (Davenport and Wong 1987). However, during the salinity preference experiments, mud crabs were only allowed 30 min to choose a salinity (Davenport and Wong 1987), which may not be a sufficient period for the mud crabs to react.

Fisheries for mud crabs are associated mostly with estuaries. Within-year variations in catch rates of mud crabs in subtropical Queensland were positively correlated with temperature and incidence of moulting (Hill 1982; Williams and Hill 1982). Williams and Hill (1982) found that catches were positively correlated with daily water temperature ($r = 0.56$, $n = 44$), but not with salinity ($r = 0.09$, $n = 44$), where salinity ranged between 24 and 35. However, small catches of mud crabs in the Gulf of Carpentaria have been attributed by commercial fishers to high migration rates of mud crabs out of fishing areas and recruitment failure occurring as a consequence of extended periods of freshwater runoff (Helmke *et al*. 1998). The downstream movement of mud crabs following floods was also reported by Stephenson and Campbell (1960) and Hill (1975) reported that heavy floods (with salinity dropping to 2) eliminated or severely reduced the number of mud crabs in two South African estuaries.

Mud crab catch has been positively correlated with summer freshwater flow in a subtropical estuary (Loneragan and Bunn 1999). Loneragan and Bunn (1999) suggested that freshwater flow might influence the catchability of mud crabs by stimulating their downstream movement away from low salinity water (thereby increasing their density in fishing grounds), and affect recruitment by reducing the competition for burrows and increasing the survival of juveniles. Increased juvenile survival would suggest that enhanced catches of mud crab could occur in the following years (i.e. a lagged effect), but lagged correlations were not examined by Loneragan and Bunn (1999).

Based on the available information in the literature, we identified that freshwater flow might influence (*i*) the catchability and (*ii*) the recruitment of mud crabs, but we have not speculated further in the exact mechanisms of this influence, given the conflicting evidence in the literature. Therefore, we examined correlations between catches of mud crabs and freshwater flow in the Fitzroy region in an exploratory manner.

Analysis of catch and freshwater flow

Our preliminary analyses aimed to determine whether there was evidence of potential relationships between catch and freshwater flow for banana prawns, barramundi and mud crabs in central Queensland and, if so, which of theoretical mechanisms generated from the life-history assessments were supported most consistently by the correlative analyses.

Fisheries catch data

Catch data were obtained from: (*i*) the Financial Year Reports of the Queensland Fish Board (QFB) from 1945 to 1980; and (*ii*) the daily commercial fisheries logbook (CFISH) of the Queensland Department of Primary Industries and Fisheries from January 1988 to June 2003. The QFB data represent fisheries catch passing through regional depots, with the majority of the fisheries catch passing through a depot being caught in the nearby area. For the QFB data, the Fitzroy region includes the Rockhampton, Yeppoon and Rosslyn Bay depots (Fig. 2). The CFISH data represent the catch (by weight or number) recorded in spatial grids of 30^2 nm ($= 1668\,km^2$). For the CFISH data, catch in the Fitzroy region was assumed to be represented by CFISH grids R28, R29, R30 and S29 (Fig. 2). Only CFISH data were used in the analysis of banana prawn catches because the QFB data pooled all prawn species (i.e. banana prawns as well as eastern king prawns) and occurred during a time when the trawl fishery was rapidly expanding in northern Australia (Fig. 3). Therefore, it was uncertain if the QFB data were an appropriate index of abundance of banana prawns. Data from the QFB and CFISH were used in the analysis of barramundi, but the datasets were analysed separately, because data for additional factors (i.e. fishing effort and stocking of fingerlings) were available and these factors potentially influenced the catches reported in the CFISH data. Annual numbers of fingerlings stocked into the Fitzroy River system were obtained from the Queensland Department of Primary Industries and Fisheries. Stocking of barramundi fingerlings to enhance recreational fisheries in freshwater impoundments has occurred in the Fitzroy River catchment since February 1990. Barramundi stocked into freshwater impoundments can move downstream to the estuary when floods cause the impoundments to overflow (Australian National Sportfishing Association, Infofish Services, Rockhampton, unpublished data). The total number of fingerlings stocked into impoundments varied between years, ranging from about 1000 to 78 000 (Fig. 3), and did not occur in some years (i.e. no stocking in 1991 or 1995). We only included stocking events into impoundments that have overflowed since 1990, because it was only individuals from these impoundments that could have contributed to the commercial catch.

Catch was aggregated into annual totals to investigate inter-year trends. However, QFB data were only available for financial year totals. CFISH data were aggregated to represent the seasonal trends in landings (as per Sobrino *et al*. 2002). For CFISH data, the starting month was September for banana prawns, but July for barramundi and mud crabs (i.e. financial year, consistent with QFB data). An additional adjustment that we made to the barramundi dataset was to exclude the data point corresponding to the 1988 financial year. We excluded the 1988 data point because this was the first year of the compulsory CFISH logbook and anecdotal reports from fishers suggested that the catch might have been under-reported.

Freshwater flow and other relevant abiotic data

Freshwater-flow data were obtained from an integrated quantity and quality model (IQQM) of the estimated end-of-system flow maintained by the Queensland Department of

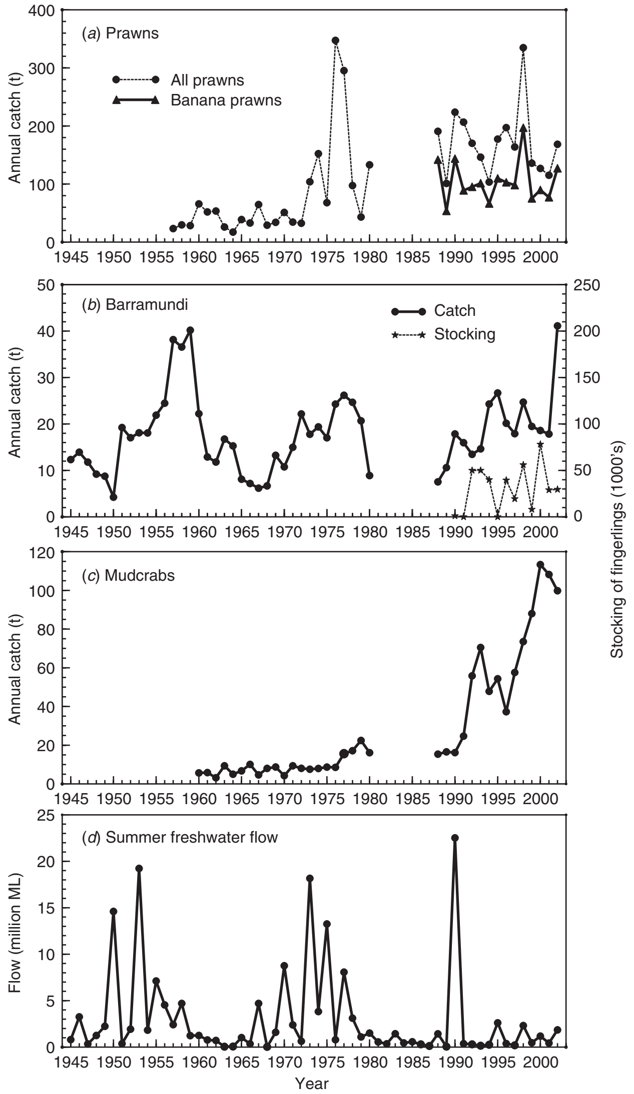

Fig. 3. Total annual catches of (*a*) all prawn species (circle) and banana prawns (triangle), (*b*) barramundi (circle) and stocked barramundi fingerlings (star), (*c*) mud crabs (circle) and (*d*) summer freshwater flow (circle) in the Fitzroy River region, Queensland. Data are from the records of the Queensland Fish Board (pre-1981) and commercial logbook (CFISH) of the Queensland Department of Primary Industries and Fisheries (post-1987).

Natural Resources. IQQM includes rainfall-runoff modelling and balances streamflow (both estimated and gauged) against water extractions to provide an estimate of the quantity of water flowing out of the 'end-of-system' i.e. that flowing into the estuary. A single source of freshwater-flow estimates was not available from 1945 to 2002. The IQQM data was only available until 1996, which is mid-way through the CFISH time series. Therefore, we used an alternative estimate of freshwater flow to the estuary: gauged streamflow at the most downstream gauging station (i.e. at 'The Gap', 142.1 km adopted middle thread distance), minus seasonal extractive uses estimated by the Queensland Department of Natural Resources and Fitzroy River Water. We considered the compatability of the two methods and, given that the differences in the estimated quantities by the two methods are inconsequential in comparison to the size of the flows in the Fitzroy River, we decided that it was better to have a relatively constant measure of the fresh water flowing to the Fitzroy River estuary for each dataset. Therefore, in the separate analysis, we used IQQM flow estimates for the QFB data (i.e. 1945 to 1980) and gauged flow minus extracted use for the CFISH data (i.e. 1985 to 2002).

The selection of freshwater-flow variables was based on the proposed causal mechanisms derived from the life-history assessment. Variables were also categorised for their effects on: (*i*) catchability (i.e. short-term, no lags, coinciding with the seasonality of the fishery); and (*ii*) recruitment (i.e. survival during the first year of life, beginning at the start of the spawning season for that species), lagged by the average time for a cohort (= year class) to recruit to the fishery. Lags were one year for banana prawns (indicated as variable^{-1}), three and four years for barramundi (indicated as variable^{-3} or variable^{-4}) and one and two years for mud crabs (indicated as variable^{-1} or variable^{-2}). No variables were categorised for their effects on productivity because of the difficulty in differentiating this effect given that we only had catch data.

Flow variables were aggregated into seasonal totals, where spring = September to November, summer = December to February, autumn = March to May and winter = June to August. For barramundi, we also included 'spawning season', which was an aggregate total of freshwater flow in spring and summer, i.e. September to February inclusive.

The additional abiotic variable of coastal rainfall was included in analyses because of the uncertainty of the proposed causal mechanisms. In the Fitzroy River estuary, 'blue sky' floods (i.e. increased freshwater flows to the estuary without coastal rainfall events) can occur because of the vast size of the catchment. Alternatively, heavy coastal rainfall can result in localised flooding of the estuarine floodplain, without increased freshwater flow occurring in the river. Rainfall variables were aggregated in the same manner as freshwater flow. Rainfall in the Fitzroy region was averaged for the nine coastal rainfall stations that were within 50 km of the coast and on the seaward side of the coastal mountain ranges (i.e. contributing to the estuarine catchment of the Fitzroy River estuary). Rainfall data were derived from the historic monthly rainfall provided in Rainman StreamFlow 4.3 (Clewett *et al.* 2003).

Analysis of data

All data were transformed ($\log_{10}(X + 1)$) before analysis to normalise the variances. Correlation coefficients were calculated between annual catch and freshwater flow and rainfall variables. All subsets general linear models (GLMs), which identify a number of 'best' models (GenStat 2000),

Table 2. Correlation coefficients (*r*) between annual banana prawn catch (adjusted for effort) and freshwater flow and rainfall in the Fitzroy Region, based on annual catches reported to CFISH, the commercial logbook of the Queensland Department of Primary Industries and Fisheries

Effect[A]	Variable	All sectors pooled (1989 to 2002)		Otter trawl (1989 to 2002)		Beam trawl (1989 to 2002)	
		Flow	Rain	Flow	Rain	Flow	Rain
R	Spring	0.07	−0.35	0.22	0.16	0.09	0.35
R&C	Summer	0.58*	0.58*	0.51	0.41	0.19	0.19
C	Autumn	−0.04	−0.03	−0.42	−0.49	−0.14	−0.35
R	Spring^{-1}	−0.54*	−0.27	−0.29	0.09	0.35	0.58*
R	Summer^{-1}	0.48	−0.36	−0.29	−0.37	0.05	−0.10
R	Autumn^{-1}	−0.15	−0.01	−0.41	0.02	0.19	−0.03

*$P < 0.05$. [A]Variables are proposed to affect recruitment (R), catchability (C) or both recruitment and catchability (R&C), because recruitment of banana prawns occurs during spring and summer and the fishery is operational in summer and autumn.

Table 3. Best all subsets regression for banana prawn catch and freshwater flow and rainfall components for the Fitzroy region, based on annual catches reported to CFISH, the commercial logbook of the Queensland Department of Primary Industries and Fisheries (1989 to 2002)

Fishery sector	Regression model[A]	Percentage variance accounted for (r^2)	Degree of autocorrelation
All combined	Effort, summer flow, spring^{-1} flow (−)	84.9	−0.033
	Effort, summer rain, spring^{-1} flow (−)	84.3	−0.126
Otter trawl	Effort, summer flow	90.7	−0.013
Beam trawl	Effort, spring^{-1} rain	84.3	−0.294

[A]Factors in the multiple regression are positively related to catch unless otherwise indicated.

were used to more thoroughly explore potential relationships between catch and the freshwater flow and rainfall variables. Correlations and the GLMs were checked for the degree of autocorrelation among the residuals and, where significant, the degrees of freedom were adjusted to account for serial autocorrelation (Pyper and Peterman 1998). Following Staunton-Smith *et al.* (2004), ridge regressions were investigated – these methods adjust for any collinearity among the independent (X) variables. As this was not a notable feature of our data (r^2 between the Xs, averaged across all models, was 0.036), the ridge adjustments had very little effect on either the degree of fit or the coefficients, so the simpler GLMs were retained.

Observed relationships between catch and freshwater flow

Banana prawns

Annual catches of banana prawns have fluctuated between 50 and 200 t (Fig. 3). Fishing effort explained a significant proportion of this variation for all sectors combined ($r = 0.83$, $P < 0.01$), the beam-trawl sector ($r = 0.90$, $P < 0.01$) and the otter-trawl sector ($r = 0.94$, $P < 0.01$). After adjusting for effort, summer flow, summer rainfall and spring^{-1} flow were significantly correlated with catch for all sectors combined (Table 2). Summer flow or rainfall accounted for 33% of the variation in the residuals for the catch and effort relationship ($r^2 = 0.33$ for the relationship between the standardised residuals and $\log_{10}$ summer flow or rainfall, $n = 14$). Summer flow was highly correlated with summer rain ($r = 0.84$). After adjusting for effort, only spring^{-1} rain was significantly correlated with catch in the beam-trawl sector and no variables were significantly correlated with catch in the otter-trawl sector (Table 2). Autocorrelation was not a feature of the banana prawn data, because the residuals of the correlations were not significantly autocorrelated.

All subsets regression identified two alternative models that explained around 84% of the variation in catch of banana prawns for all sectors combined (Table 3). The models contained summer flow (or rainfall) and spring^{-1} flow. Multiple-regression models explained around 91% and 84% of the variation in the catch of banana prawns for the otter-trawl and beam-trawl sectors respectively (Table 3). Summer freshwater flow was significant in models for all sectors combined and the offshore otter-trawl sector, but not for the estuarine-based beam-trawl sector, where spring^{-1} rain was a significant factor in the model. The spatial distribution of the beam-trawl sector compared to the otter-trawl sector adds to the complexity of interpreting these results, because the beam- and otter-trawl sectors target different life

Table 4. Correlation coefficients (*r*) between annual barramundi catch and freshwater flow, rainfall, and stocking for the Fitzroy region based on annual catches reported to the Queensland Fish Board and CFISH, the commercial logbook of the Queensland Department of Primary Industries and Fisheries

Effect[A]	Variable	Queensland Fish Board (1945 to 1980)		CFISH (1989 to 2002)	
		Flow	Rain	Flow	Rain
C	Spring	0.05	−0.10	−0.38	−0.47
C	Summer	0.19	0.36	0.64*	0.67*
R	Spring^{-3}	0.31	0.21	−0.11	0.13
R	Spring^{-4}	0.24	0.18	0.25	−0.03
R	Summer^{-3}	0.49*	0.46*	−0.39	−0.30
R	Summer^{-4}	0.44*	0.44*	0.31	0.25
R	Autumn^{-3}	0.42*	0.09	0.44	0.05
R	Autumn^{-4}	0.23	0.05	0.05	−0.24
R	Winter^{-3}	0.21		0.33	
R	Winter^{-4}	0.27		−0.07	
R	Stocking^{-3}			0.45	
R	Stocking^{-4}			0.25	

*$P < 0.05$. Critical values for correlation coefficients (r) for the Queensland Fish Board data were based on the adjusted degrees of freedom to account for serial autocorrelation as per Pyper and Peterman (1998). Autocorrelation was not a feature of the CFISH data, after catch had been adjusted for effort. [A]Variables are proposed to affect recruitment (R) or catchability (C).

stages (i.e. juveniles in the estuary *v.* adults in offshore waters respectively). Our results lend some support to the theory that summer flows affect the distribution of banana prawns, with higher flows stimulating prawns to move downstream and out of estuaries, thereby increasing the catch of offshore fisheries (Glaister 1978; Vance *et al.* 1985). However, interpretation of our results is complicated by the conflicting direction of impact of spring^{-1} flow and spring^{-1} rain, which have a negative and positive effect on total catches and beam-trawl catches respectively.

Barramundi

Annual catch of barramundi has fluctuated between four and 40 t between 1945 and 2002, with a notable 15- to 20-year cycle in the data (Fig. 3). For the QFB data (i.e. 1945 to 1980), catch of barramundi was significantly correlated with summer flow or rainfall lagged by three or four years (i.e. summer^{-3} or summer^{-4}) and autumn^{-3} flow (Table 4). Autocorrelation was a feature of the QFB data, so critical values for the correlation coefficient (r) were based on the adjusted degrees of freedom to account for serial autocorrelation (Pyper and Peterman 1998). For the CFISH data (i.e. 1989 to 2002), fishing effort explained a significant proportion of the variation in catch ($r = 0.76$, $P < 0.01$). After adjusting for effort, summer flow and rainfall in the same year as the catch were significantly correlated with barramundi catch, but no lagged variables were significant (Table 4). Autocorrelation was not a feature of the CFISH data, once barramundi catch had been adjusted for effort.

All subsets regression identified a number of alternative models that explained about 38% of the variation in the QFB barramundi catch and about 87% of the variation in the CFISH barramundi catch (Table 5). The inclusion of effort in the regression models of the barramundi catch (i.e. for the CFISH data) was the main driver for the increased fit of the multiple linear models. Variables in the models from both datasets (i.e. QFB and CFISH) are consistent with the theoretical mechanisms proposed in the life-history assessment, with summer rain having a positive effect on catchablity and summer flow or rain lagged by three or fours years having a positive effect on recruitment (i.e. year-class strength). And as you might expect, the stocking of fingerlings in impoundments that have overflowed appears to have a lagged effect on commercial CFISH catches in the estuary. The role of autumn^{-3} flow and winter^{-4} flow is not obvious from the life-history assessment, although positive effects on recruitment are possible, albeit via an unknown mechanism. This might be a Fitzroy-specific relationship, as this estuary is at the lower limit of the distribution of barramundi, with fish kills being associated with unusually low winter temperatures.

Our preliminary results suggest that summer flow or rainfall influences the catch of barramundi immediately and in subsequent years (i.e. lagged by three or four years) and, at least in the Fitzroy River estuary, these relationships are consistent over time (i.e. 1945 to 2002), despite several events in the study area that may have caused major system changes. These included: (*i*) a major change to the hydrology of the Fitzroy River in 1991, when a 10-km loop of the river was eliminated during a 1-in-100-year flood; (*ii*) the stocking of barramundi fingerlings into various freshwater habitats in the catchment from 1992, although stocking is a factor included the analyses of the CFISH data; (*iii*) upgrading of the fishway

Table 5. Best all subsets regression for barramundi catch and freshwater flow and rainfall components for the Fitzroy Region based on annual catches reported to the Queensland Fish Board (QFB, 1945 to 1980) and CFISH (1989 to 2002), the commercial logbook of the Queensland Department of Primary Industries and Fisheries

Data source	Regression model[A]	Percentage variance accounted for (r^2)	Degree of autocorrelation
QFB	Summer^{-3} flow, summer^{-4} flow, summer rain	38.65	0.216
	Autumn^{-3} flow, summer rain, winter^{-4} flow	38.37	0.125
	Autumn^{-3} flow, summer rain, summer^{-4} rain	38.79	0.157
	Summer^{-3} flow, summer^{-4} rain, summer rain	37.89	0.132
CFISH	Effort, summer rain, summer^{-4} rain, stock^{-4}	88.02	0.091
	Effort, summer rain, summer^{-4} flow, stock^{-4}	86.98	−0.068

[A]Factors in the multiple regression are positively related to catch unless otherwise indicated.

Table 6. Correlation coefficients (r) between annual mud crab catch and freshwater flow and rainfall in the Fitzroy region based on annual catches reported to the Queensland Fish Board and CFISH, the commercial logbook of the Queensland Department of Primary Industries and Fisheries

Effect[A]	Variable	Queensland Fish Board (1960 to 1980)		CFISH (1988 to 2002)	
		Flow	Rain	Flow	Rain
C	Spring	−0.15	−0.40	0.30	0.19
C	Summer	−0.38	−0.46*	0.38	0.11
C	Autumn	−0.63**	−0.10	−0.35	−0.36
R	Spring^{-1}	−0.32	−0.32	0.07	0.01
R	Spring^{-2}	0.36	0.17	0.47	0.26
R	Summer^{-1}	−0.07	0.05	0.02	−0.21
R	Summer^{-2}	0.08	−0.25	0.20	0.19
R	Autumn^{-1}	0.18	0.23	0.05	0.14
R	Autumn^{-2}	0.14	0.46*	0.70**	0.23

*$P < 0.05$, **$P < 0.01$. Autocorrelation was not a feature of the Queensland Fish Board data, after catch had been adjusted for year, or the CFISH data, after catch had been adjusted for effort. [A]Variables are proposed to affect recruitment (R) or catchability (C).

on the barrage in 1994 to enable migration of fish (Stuart and Mallen-Cooper 1999); and (*iv*) various changes to fisheries management and marketing arrangements, possibly altering patterns of fishing.

Mud crabs

Reported catches of mud crabs in the Fitzroy region have dramatically increased from around 5 t in 1960 to 100 t in 2002. We speculate that this increase is probably a consequence of increased fishing effort in the region and more accurate reporting of catch data. Autocorrelation was not a feature of the QFB mud crab catch, once catch had been adjusted for year ($r = 0.75$, $P < 0.001$), as per Loneragan and Bunn (1999). The QFB catch of mud crabs adjusted for year was significantly negatively correlated with autumn flow and summer rain, but was significantly positively correlated with autumn rain lagged by two years (i.e. autumn^{-2} rain, Table 6). Fishing effort explained most of the variation in CFISH mud crab catches ($r = 0.97$, $P < 0.01$). After adjusting for effort, autumn flow lagged by two years (i.e. autumn^{-2} flow) was the only variable significantly correlated with mud crab catch (Table 6).

All subset regression identified several alternate models that explained between 70 and 97% of the variation in mud crab catch for the QFB and CFISH data respectively (Table 7). Although multiple-term models could be fitted, they only had a slight improvement on the 'simpler' models of year and autumn flow (QFB data, adjusted $r^2 = 70.91$) or effort and autumn^{-2} flow (CFISH data, adjusted $r^2 = 96.70$).

Implications of correlation analyses

Banana prawns

The results of the correlation analyses for the central Queensland area concur with other studies that catches of banana prawns, particularly in offshore otter-trawl fisheries, are related to summer freshwater flows. The total catch of

Table 7. Best all subsets regression model for mud crab catch and freshwater flow and rainfall components for the Fitzroy region, based on annual catches reported to the Queensland Fish Board (QFB, 1945 to 1980) and CFISH, the commercial logbook of the Queensland Department of Primary Industries and Fisheries (1988 to 2002)

Data source	Regression model[A]	Percentage variance accounted for (r^2)	Degree of autocorrelation
QFB	Year, autumn flow	70.91	0.191
	Year, spring rain (−), spring^{-1} rain (−), spring^{-2} flow	77.13	−0.074
	Year, spring^{-1} rain (−), spring rain (−), autumn^{-1} flow	77.00	−0.019
	Year, spring rain (−), summer rain (−), spring^{-2} flow	73.71	−0.132
CFISH	Effort, autumn^{-2} flow	96.70	0.163
	Effort, autumn rain (−), spring^{-2} rain, spring rain	96.72	0.162

[A]Factors in the multiple regression are positively related to catch unless otherwise indicated.

banana prawns increases in proportion to summer freshwater flow. The temporal and spatial aspects of the correlation support the proposed hypothesis that freshwater flow affects their catchability and possibly recruitment. Further within-year analyses of commercial catch data may provide stronger evidence of recruitment effects, but such analyses were beyond the scope (and length) of this paper. Browder *et al.* (2002) recommended further research into the seasonal and annual patterns of the availability of post-larval prawns to provide greater evidence that freshwater flows increase the abundance or biomass of prawns as a consequence of improved growth and survival through trophic cascading. It is unlikely that correlative analyses would provide evidence of such productivity related effects. Therefore, further research into the freshwater-flow requirements of banana prawn fisheries may need to use empirical data collected at a scale different to that of simply the quantity of commercial catch. Whether such data are fishery-dependent (i.e. size-class structure and length–frequency analysis) or fishery-independent (i.e. relative densities of post-larval and juvenile banana prawns) will depend on the theoretical mechanism (of the role of freshwater flow) being investigated.

Barramundi

We cannot attribute causality to the observed relationships or to changes in these relationships because our assessment is based on correlations. However, the within-year influence of freshwater flow on barramundi catches supports the proposed hypotheses of the effect of flow on catchability and concurs with anecdotal reports by commercial fishers. The significant correlations between catch and flow or rainfall lagged by three or four years in both datasets provides consistent quantitative evidence in support of the positive influence of freshwater flow on recruitment for barramundi suggested by Dunstan (1959) and (Williams 2002). In the first year of life, post-larval barramundi exploit swamps, coastal lagoons and other supralittoral habitats, which are thought to offer sheltered, highly productive nursery habitats that allow rapid growth and enhanced survival (Davis 1985; Russell and Garrett 1983, 1985). Access to these habitats is via tidal inundation and freshwater runoff from localised rainfall. The life-history assessment and some of the correlative analyses support previous assertions that barramundi in tropical Australia have freshwater-flow requirements. However, barramundi populations are adaptable to the prevailing conditions, with the life cycle varying across the species' distribution. For example, diadromy is facultative (Russell 1990; Pender and Griffin 1996) and cannibalism effects on recruitment rates have been reported in some areas (Walters *et al.* 2001). Further research is needed to clarify how recruitment and productivity are enhanced as a consequence of increased freshwater flow, in particular the timing of these flows, their magnitude, the mechanism by which the effects occur (including habitats affected) and whether the relationship is linear or a threshold. Outcomes of such research will need to be adapted for each estuary in tropical Australia to take into account the specific hydrogeographic conditions and life-cycle adaptations. Our current findings led us to investigate the influence of freshwater flow on the year-class strength of barramundi in the Fitzroy River estuary. Results from an age-based index of year-class strength confirmed that recruitment was strongly correlated to freshwater flow in summer and spring (see Staunton-Smith *et al.* 2004 for details).

Mud crabs

The observed correlations between catch and freshwater flow (adjusted for year or effort, depending on the dataset) provide ambiguous, albeit preliminary, results as to the effects of freshwater flow on mud crabs. This may be a consequence of the reported catch data not being an appropriate index of the abundance of mud crabs in the Fitzroy region, particularly between 1960 and 1980 (i.e. the QFB data). From the CFISH data, there is evidence that freshwater flows in autumn may affect the recruitment (i.e. cohort or year-class) strength of mud crabs, which concurs with the suggestion of recruitment effects by Loneragan and Bunn (1999). However, the biological link between autumn flows and the life history of mud crabs requires further investigation, perhaps into the hypothesis that recruitment effects are related to burrow competition.

Productivity effects

From the analysis of annual catch data, we found it difficult to identify or determine the level of importance of proposed productivity effects of freshwater flow in estuaries that result from trophic linkages via changes in primary or secondary production (Drinkwater and Frank 1994). Productivity effects (e.g. growth) are not independent of recruitment effects (e.g. survival), and they occur at similar temporal scales. Investigation of trophic linkages hypothesised to occur as a consequence of nutrient input associated with freshwater inflow requires data for several levels of the estuarine food web, collected at appropriate spatial and temporal scales (e.g. Livingston *et al*. 1997; Kimmerer 2002*a*). As an example, Kimmerer (2002*a*) concluded that variation in the abundance of organisms at higher trophic levels was more likely to be a consequence of changes in the physical habitat associated with freshwater flow, than with upward trophic transfer. An alternative to such detailed studies may be to correlate growth rates of individual species with freshwater flow. Preliminary investigations of barramundi growth rates in the Fitzroy River estuary suggest a significant positive relationship between growth rates and freshwater flow to the estuary (Sawynok 1998; J. B. Robins, unpublished data), providing initial evidence in support of the productivity hypothesis, at least for one of the major estuarine fish species in tropical Australia.

Freshwater-flow requirements of estuarine fisheries in tropical Australia

The relationships between estuarine fisheries production and freshwater flow reported within this paper provide quantitative evidence that estuarine fisheries in tropical Australia are related to freshwater flow. Determining whether these relationships are consistent with other tropical estuaries is an issue requiring further research. Correlative analyses would be a starting point, but improved knowledge of the role of freshwater flow in tropical Australian estuaries would assist in determining how freshwater flows affect the catchability, recruitment or productivity of estuarine fisheries species.

It is uncertain whether other tropical estuarine species have similar freshwater-flow requirements to that of banana prawns, barramundi or mud crabs. However, we suggest that for most fishery species, freshwater-flow requirements could be considered in terms of the effects on catchability, recruitment (i.e. cohort or year-class strength) and productivity.

Catchability is likely to be related to the seasonality of the fishery, and therefore freshwater flows preceding, or occurring during, the main fishing season may have the most influential effects. We have grouped freshwater-flow effects on recruitment as those occurring during the first year of life for species that live longer than one year, or its equivalent in shorter-lived species (e.g. banana prawns). There may be several critical times during this period when the survival of a species is enhanced by freshwater flow. However, parts of Australia have a highly variable climate and, consequentially, a variable flow regime. It may be that estuarine fishery species are able to take advantage of windows of opportunity when good conditions for recruitment occur. (For a discussion of how this pertains to barramundi see Davis (1985), Russell and Garrett (1985) and Griffin (1987).) Therefore, freshwater flows that enhance recruitment may not be temporally limited outside the need for such flows to coincide approximately with the spawning season, which is extended in many tropical species.

Effects of increased freshwater flow on estuarine productivity are likely to be observed as increased growth rates, which theoretically may lead to greater survival of individuals and/or increased biomass of the population. Another area requiring research is determining the mechanisms by which estuarine productivity is enhanced through increased freshwater flow, and how (and whether) this productivity is progressed up the food chain.

Knowledge of the freshwater-flow requirements of estuarine fisheries has increased substantially since the issue was raised in the scientific literature in the 1950s, 1960s and 1970s. Although estuarine issues are being increasingly identified as being important in the documentation associated with water planning and development, lack of knowledge or suitable methods are hampering the ability of managers to effectively include the needs of estuarine fisheries. Coalescence of available knowledge supported by further research and analysis is needed to better quantify the required freshwater flows.

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