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Direct and Indirect Interactions Between Lower Estuarine Mangrove and Saltmarsh Habitats and a Commercially Important Penaeid Shrimp

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Abstract Vegetated habitats in estuaries may provide a structural refuge and food supply in the same place, but benefits are also derived where a productive food source and suitable habitat are adjacent to each other. Quantifying these relationships is fundamental to understanding the structural and functional characteristics of estuarine ecosystems and for informing management actions. Effective juvenile habitat (habitat that contributes greater-than-average numbers of recruits to the adult population), recruitment patterns and trophic relationships were studied for Eastern King Prawn (*Penaeus plebejus*) in the lower Clarence River estuary, New South Wales, between 2014 and 2016. Effective juvenile habitat was identified in both the north arm and main river channel of the estuary, and these areas also supported a higher abundance of juvenile prawns. There was minimal recruitment to the southern channels of the estuary, possibly due to reduced connectivity with the incoming tide arising from a rock wall. Trophic relationships in parts of the lower estuary were evaluated using stable isotopes, and saltmarsh grass (*Sporobolus virginicus*) was the dominant primary producer supporting juvenile Eastern King Prawn productivity across the area. Mangroves were of minimal importance, and seagrass cover was minimal in the area studied. The patterns observed indicate that nursery function of different areas within the lower estuary is a product of connectivity, recruitment and nutrition derived from primary productivity of vascular plants. Habitats within the lower Clarence River estuary have seen substantial degradation over decadal time scales, and the implications of our findings for targeting future habitat repair are discussed.

Keywords Nursery habitat · Effective juvenile habitat · Fisheries productivity · Stable isotope · Penaeidae · *Penaeus plebejus* · Clarence River

Introduction

Estuaries represent some of the most productive environments in the world and support a range of ecosystem services (Costanza et al. 1997). A large proportion of the value derived from estuarine systems occurs through the support of exploited aquatic species, through some or all of their life history stages (especially juveniles, Lenanton and Potter 1987; Elliott et al. 2007). The role of estuarine habitats during these early life history stages has led to the development of the nursery habitat paradigm (Beck et al. 2001), and diverse studies have compared and contrasted the relative values of different estuarine habitats for numerous aquatic species.

Food and refuge are two of the most important attributes that estuaries provide for the early life history stages of aquatic animals. Vegetated habitats in estuaries may provide a structural refuge and food supply in the same place (Ochwada et al. 2009; Becker et al. 2010), but benefits are also derived where a productive food source and suitable habitats are adjacent (Ahrens et al. 2012). Saltmarsh habitats are a good example of this, potentially providing protection from predation alongside a productive food web (Boesch and Turner 1984), and this ultimately supports rapid growth and higher survival through vulnerable early life history stages (Haas et al.

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2004). The net impact of such habitats, resulting in improved survival and productivity of exploited species that rely on them (such as penaeid shrimp) can be rather compelling (e.g. Turner 1977). Because estuaries typically contain a mosaic of habitats, establishing the relative importance of different areas or habitats within an estuary is fundamental to identifying the structural and functional characteristics of estuarine ecosystems, and also to effectively target management measures among estuarine habitats to achieve the best fisheries outcomes.

Penaeid prawns (shrimp) support some of the world's most economically valuable fisheries. Many penaeids have a biphasic life cycle, which includes an estuarine (juvenile) phase and an oceanic (adult) phase (Dall et al. 1990). During the estuarine phase, saltmarsh habitats, especially the subtidal channels and pools within them, support high abundances of juvenile penaeid shrimp (e.g. Zimmerman and Minello 1984; Zimmerman et al. 1984; Minello et al. 2003; Minello and Caldwell 2006). The advent of stable isotope ecology has enabled quantitative studies of trophic linkages among saltmarsh, mangrove and exploited species. Recent work shows that food webs in or near saltmarshes and mangroves are supported by many primary producers (e.g. Melville and Connolly 2005; Sheaves et al. 2007). A combined focus on both habitat (i.e. quantitative measurements of abundance) and food webs within a seascape framework (e.g. Nagelkerken et al. 2015) can lead to powerful conclusions regarding relative nursery value (Fry and Ewel 2003).

Eastern King Prawn (*Penaeus plebejus*, EKP) is a valuable penaeid species occurring along the eastern Australian coast. Postlarval prawns recruit to estuarine nursery habitats from early summer, where they grow rapidly through their juvenile phase and undertake a synchronous emigration from estuarine nursery habitats during the last quarter of the lunar phase (most commonly during the January to March lunar months, Dakin 1938; Racek 1959; Taylor et al. 2016). Most prawns have left the estuary by mid-autumn and, as they mature, migrate north across several degrees of latitude toward the spawning grounds (Ruello 1975; Montgomery 1990). Larger estuaries in New South Wales (Australia) which contribute to fisheries productivity, often have significant areas of mangrove and intertidal saltmarsh (Saintilan and Wen 2012). The high value of Eastern King Prawn (and other penaeids) has led to recommendations for estuarine habitat repair targeted to benefit these species (see Creighton et al. 2015; Taylor 2016). There is, however, a need to better quantify the nursery role of different habitats for this species, to prioritise and target areas for rehabilitation. This study aimed to assess the importance and contribution of different habitats in the lower Clarence River estuary for Eastern King Prawn. This included the following:

1. A broad-scale assessment of the contribution of several areas across the lower estuary to the adult Eastern King Prawn stock
2. Estimation of Eastern King Prawn abundance in and around saltmarsh, mangrove and other habitats, in the lower estuary
3. Determination of the contribution of primary productivity from saltmarsh and mangrove habitats to Eastern King Prawn in the lower estuary

Materials and Methods

Study Area

The Clarence River estuary (−29.43, 153.37) is the largest estuarine system in New South Wales and is classified as a mature wave-dominated barrier estuary (Roy et al. 2001). The river is fed by a number of tributaries mainly in the upper floodplain, and the middle and lower estuary includes numerous islands north and south of the main river channel (Fig. 1). Prominent features of the lower estuary include Lake Wooloweyah in the south and North Arm in the north (Fig. 1). Lake Wooloweyah is an expansive shallow lake connected to the river by a series of narrow channels between deltaic islands that formerly comprised extensive saltmarsh (dominated by Salt Couch, *Sporobolus virginicus*) and mangrove (dominated by Grey Mangrove, *Avicennia marina*) habitats, but much of which is now reclaimed or degraded. The lake itself represents important commercial trawling grounds for School Prawn (*Metapenaeus macleayi*), and in the early twentieth century, it contained large beds of seagrass (*Zostera* sp. and *Halophila* sp.) which are now almost non-existent. North Arm is fed directly from Main Channel near the mouth and similarly contains a series of low-lying deltaic islands covered in saltmarsh and mangrove, interspersed with a network of shallow channels (Fig. 1). Just inside the entrance of the estuary, a rock wall has been constructed which directs the bulk of tidal flow up Main Channel and North Arm (Fig. 1; two small breaks in the wall allow for navigation by small vessels). Consequently, most of the tidal flow initially bypasses the downstream channel system connecting Lake Wooloweyah to the mouth, favouring Main Channel and to a lesser extent North Arm (Fig. 1).

Broad-Scale Assessment of Putative Nursery Habitat Areas

Spatial variation in stable isotope composition was used in a broad-scale assessment of the relative contribution of different areas within the lower estuary to the adult component of the Eastern King Prawn population, following Taylor et al.

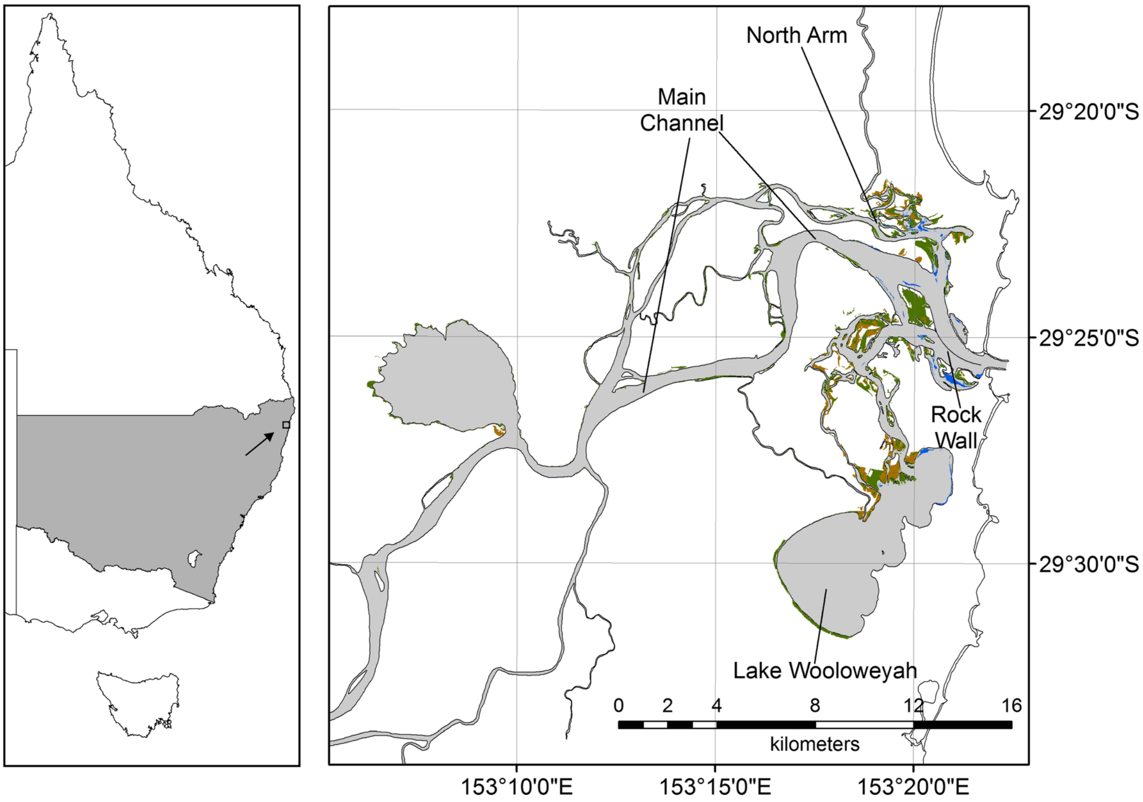

Fig. 1 Map of lower Clarence River estuary region with main features labelled. Waterway area (grey), mangrove (green), saltmarsh (brown) and seagrass (dark blue) habitats indicated

(2016). This approach exploits the species' abrupt migrations from nursery habitats within the estuary to the ocean (which coincide with the last quarter of the lunar phase, Racek 1959) and thus uses prawns emigrating from the estuary as a proxy for individuals moving from the estuarine nursery to the adult component of the population. Prawns are first captured from putative nursery areas throughout the estuary to characterise the isotopic composition specific to that area. Emigrating prawns come from nursery areas throughout the estuary and are captured near the mouth as they run to sea and matched back to putative nursery areas on the basis of isotopic similarity (Taylor et al. 2016). This allows contributions of various putative nursery areas to be estimated.

To determine the isotopic composition of different areas across the estuary, juvenile Eastern King Prawn were sampled across 12 putative nursery areas in the lower estuary during early February 2014, using up to four ~ 100-m tows of a sled net (see description of gear below). Emigrating Eastern King Prawn were collected by commercial trawler as they exited the mouth of the estuary, with sampling conducted over six nights during the last quarter of the lunar phase in the January and February lunar months, when emigration is greatest, in 2014. For prawns captured in putative nursery areas, three composite samples containing equal quantities of muscle tissue from six individual prawns were prepared for stable isotope analysis. All prawns captured from the mouth of the estuary were prepared as individual samples for analysis (i.e. not composite samples). Muscle tissue was rinsed in distilled water for 10 min, dried at 60 °C for ~ 48 h and isotopic composition (^{15}N and ^{13}C) measured on a Sercon 20-20 isotope ratio mass spectrometer (IRMS, Cheshire, UK). Measurement precision was determined through repeated measurements of internal standards and was ±0.11 and ±0.17‰ for $\delta^{15}N$ and $\delta^{13}C$, respectively. Isotopic composition was expressed as a delta value relative to international standards using conventional methods (Fry 2006).

A distance-based approach was used to assign emigrating Eastern King Prawn to putative nursery habitat areas across the lower Clarence River estuary. The specific isotopic turnover rate for Eastern King Prawn has not yet been determined; however, 8–10 weeks is a likely time range for a new isotopic signature to be reflected in prawn muscle. To avoid making unlikely assignments, a point-in-polygon simulation (Smith et al. 2013) was applied to the dataset. This assessed the completeness of isotopic data from putative nursery habitat areas for assigning the set of emigrating prawns and used to exclude emigrating prawns from assignment (i.e. assignment was not attempted) whose source area was not reflected in the isotope map. Non-excluded emigrating prawns were assigned to putative nursery habitat areas as follows. The isotopic composition of each putative nursery habitat area was specified as a normal distribution, based upon the composite samples of juvenile Eastern King Prawn analysed from each area. In each simulation, the distribution of values from each putative nursery habitat area was randomly sampled and used to calculate the Euclidian distance between the emigrating prawn and the putative nursery habitat areas in bivariate (i.e. C and N) isotopic space. For each emigrating prawn in each simulation, a binomial response was returned: "1" for the putative nursery habitat area that was closest to the emigrating prawn in bivariate isotopic space and "0" for all other putative nursery habitat areas. One thousand simulations were conducted for each emigrating prawn and the associated binomial probability calculated for each habitat. The putative nursery habitat area with the greatest probability was selected as the most likely source habitat for that emigrating prawn. The assignment data were also used to determine whether each area could be considered an effective juvenile habitat (EJH), using the classification approach of Dahlgren et al. (2006). This approach designates EJH as areas that contribute more to the adult population than the average of contributions across all areas. All isotope modelling was undertaken using a custom script written in Matlab (Mathworks, Natick, MA, USA).

Determination of Prawn Abundance Across the Lower Estuary

We then sought to determine patterns in Eastern King Prawn abundance across important areas identified from the broad-scale analysis described above. Twenty sites within these important areas in the lower estuary (some corresponding with the putative nursery habitats described above) were sampled in December 2015 and February 2016 (these time points span the period where juvenile Eastern King Prawn are most abundant within estuarine nurseries). Each site was sampled after dusk using a sled net (0.75 × 0.45-m mouth, 4-m length, 26-mm diamond mesh body and 6-mm octagonal mesh cod-end, see Taylor et al. 2017) in last quarter of the moon. Four ~ 100-m tows were undertaken at each site on each sampling date, with a GPS waypoint marked at the start and finish of each tow (to calculate tow length). Water depth, temperature, salinity, dissolved oxygen and turbidity were recorded at each site during each sampling time. Samples were immediately placed on ice and then later frozen. Each sample was sorted, and all penaeid prawns were identified and counted. The dimensions of the gear, the actual length of each tow and gear efficiency estimates (0.48; M.D. Taylor, unpublished data) were used to standardise abundance estimates to number-EKP-per-hundred-square-metres (no. EKP 100 m^{-2}). Abundance data were analysed using Geostatistical Analyst in ArcMap v. 10.2.2 (Environmental Science Research Institute, California, USA). A predicted surface showing relative juvenile Eastern King Prawn abundance across the survey areas was computed from standardised point abundance data (derived from sled tows) with a fifth-order global polynomial interpolation (GPI).

Contribution of Potential Food Sources to Eastern King Prawn Diet

Several potential basal sources (referred to as "sources" below) were identified for Eastern King Prawn and collected from areas 6, 7, 8 and 10 (from the broad-scale assessment) in December 2015 and March 2016. These included *S. virginicus* (Saltwater Couch), *Suaeda australis* (Austral Seablite), *Avicennia marina* (Grey Mangrove) and mangrove pneumatophore epiphytes, microphytobenthos and fine benthic organic matter (MPB/FBOM) and particulate organic matter (POM). MPB/FBOM, which includes detritus, microphytobenthos, sediment and other biological material, was separated from bulk sediment by sieving following the method of Saintilan and Mazumder (2010) and then sent for stable isotope analysis. POM samples were obtained by filtering 1 L of water onto a pre-combusted (450 °C for 24 h) glass fibre filter paper (GF/C) under low vacuum and then dried at 60 °C for 24 h before being placed in a glass vial for stable isotope analysis. For Eastern King Prawn, muscle tissue was excised from the tail for stable isotope analysis. All plant and animal samples were rinsed with deionised water and placed in individual HCl-rinsed glass petri dishes, dried at 60 °C for 24 h and then ground to a fine powder using a Retsch Mixer Mill MM200. Ground samples were placed in aluminium capsules (6–8 mg for plant material and 1–2 mg for animal tissue) and sent to Griffith University, Queensland, for stable isotope analysis using a Sercon Hydra 20-22 automated Isoprime Isotope Ratio Mass Spectrometer. The standard used to compare carbon isotope content was Pee Dee Belemnite Limestone Carbonate, and stable isotope composition was expressed in delta-notation using conventional formulae (Fry 2006).

Mean $\delta^{13}C$ values ($n \geq 3$) were calculated for Eastern King Prawn and all food sources at each site. These mean values were used in the IsoSource model of Phillips and Gregg (2003) to calculate feasible food source combinations that could explain the prawn stable isotope signatures. The IsoSource model examines all possible combinations of each food source (0–100%) in 1% increments and reports the feasible solutions for each taxon as a distribution, mean, maximum, minimum and 1 and 99 percentiles. Although samples were also analysed for $\delta^{15}N$, only $\delta^{13}C$ was used in the IsoSource modelling. Mean isotope values of consumers need to be corrected for trophic fractionation prior to running the IsoSource model. Trophic fractionation is much larger and uncertain for $\delta^{15}N$ than $\delta^{13}C$ (e.g. Peterson and Fry 1987), and the fractionation value for $\delta^{15}N$ is known to vary considerably with animal age, growth rates and food quality (Vander Zanden and Rasmussen 2001). For this reason, the potential contribution of food sources to consumer diet was calculated only using $\delta^{13}C$ (with a 1‰ correction) following earlier studies in Australian systems that used a similar design (see Melville and Connolly 2005; Connolly and Waltham 2015).

Results

Broad-Scale Assessment of Putative Nursery Habitat Areas

Average carbon isotopic composition was correlated with the location of putative nursery habitat areas along the estuary (Fig. 2, $F_{1,\ 11} = 19.98$, $P = 0.001$, $R^2 = 0.67$). In Lake Wooloweyah (areas 1 and 2), putative nursery habitat areas were depleted in ^{15}N relative to other areas that were a similar distance from the sea (e.g. area 9; Fig. 2), but in general, ^{15}N was enriched and ^{13}C was depleted with increasing distance from the mouth. The point-in-polygon simulation indicated that nine of the 77 emigrating Eastern King Prawn which were analysed for stable isotope composition should be excluded from assignment (Fig. 2). The remaining emigrating Eastern King Prawn showed highly asymmetric patterns in assignment among putative nursery habitat areas. Of the 12 areas sampled, the vast majority of emigrating prawns were assigned to the main marsh/mangrove areas in the North Arm (area 8; Fig. 3 and Table 1). The remaining prawns were assigned to areas within the main river channel (areas 10 and 11; Fig. 3 and Table 1), and no prawns were assigned to areas within the south arm of the estuary or Lake Wooloweyah. Using the approach of Dahlgren et al. (2006), only areas 8 and 11 were designated as EJH (Table 1).

Abundance of Eastern King Prawn Across the Lower Estuary

Eastern King Prawn were generally the most abundant epibenthic species across the lower estuary, except in the southern channels and Lake Wooloweyah. Eastern King Prawn mean (± SE) abundance was 76 ± 6 EKP 100 m^{-2} (size range 3–20 mm carapace length), with a maximum abundance of 499 EKP 100 m^{-2}. The interpolated surface across the lower estuary (bounded by the sampling area) indicated that juvenile Eastern King Prawn were most abundant 8–12 km from the mouth in the Main Channel and North Arm (Fig. 4). This included areas adjacent to the marsh/mangrove habitats in North Arm and the mangrove habitats in Main Channel (see Fig. 1).

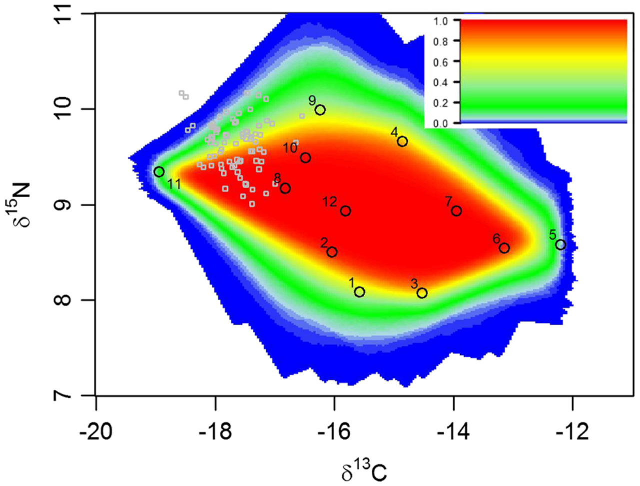

Fig. 2 Isotope biplot and simulated contours indicating completeness of putative nursery habitat area isotopic data (open circles; numbers correspond to Fig. 3 and Table 1) for assigning emigrating Eastern King Prawn (squares). Colouring indicates simulated probability (see scale bar) that habitat isotopic data reflects emigrating prawns origin. Emigrating prawns were excluded from assignment if outside the 5% (green) contour, as habitat isotopic data did not encompass the likely source

Contribution of Basal Sources of Nutrition to Eastern King Prawn

At all areas sampled, potential trophic sources were well separated in isotopic space (Fig. 5). The saltmarsh plant *S. australis* had the lowest δ^{13}C in area 10 (−28.5 ± 0.1‰) and area 6 (−28.5 ± 0.1‰), mangrove was lowest in area 8 (−30.3 ± 0.4‰) and area 7 (−29.7 ± 0.3‰) and the saltmarsh grass *S. virginicus* was most enriched in ^{13}C across all areas (−15.1 to −14.5‰, Fig. 5). For δ^{15}N, *S. virginicus* had the lowest values (0.2 to 1.9‰) in all areas and POM had the highest values in area 10 (4.9 ± 1.0‰) and area 8 (4.0 ± 1.8‰), MPB/FBOM in area 7 (3.5 ± 0.4‰) and mangrove/MPE in area 6 (5.1 ± 0.5‰, Fig. 5). For Eastern King Prawn ($n = 58$), δ^{13}C ranged over 7.2‰ and δ^{15}N ranged over 1.6‰. Area 10 was the only location sampled in both December 2015 ($n = 5$) and March 2016 ($n = 14$), and at this location, there was a significant increase in δ^{13}C from −19.4 ± 1.5 to −16.3 ± 0.2‰ ($F_{1,\ 19} = 20.215$, $P < 0.001$) and δ^{15}N from 7.8 ± 0.6 to 9.6 ± 0.2‰ ($F_{1,\ 19} = 11.543$, $P = 0.001$) over that time (Fig. 5a). In March 2016, when all areas were sampled, Eastern King Prawn in area 8 had the lowest δ^{13}C (−17.2 ± 0.2‰) and δ^{15}N (8.2 ± 0.1‰; Fig. 5b) and the highest δ^{13}C (−14.4 ± 0.1‰) and δ^{15}N (9.8 ± 0.2‰) were in area 6 (Fig. 5d).

The contributions of potential food sources to Eastern King Prawn were calculated for each area on the basis of δ^{13}C. The saltmarsh plant *S. virginicus* was the dominant source of nutrition across all sites (47–97%; Fig. 6). MPB/FBOM was the second most important nutrition source (2–11%; Fig. 6). The relative proportion of each potential food source at area 10 changed slightly between December 2015 to March 2016, with *S. virginicus* making a greater proportional contribution to the diet during March 2016 (47 vs. 75%; Fig. 6).

Discussion

General Comments

The observed distribution patterns indicated that the lower estuary was important for Eastern King Prawn, with the areas

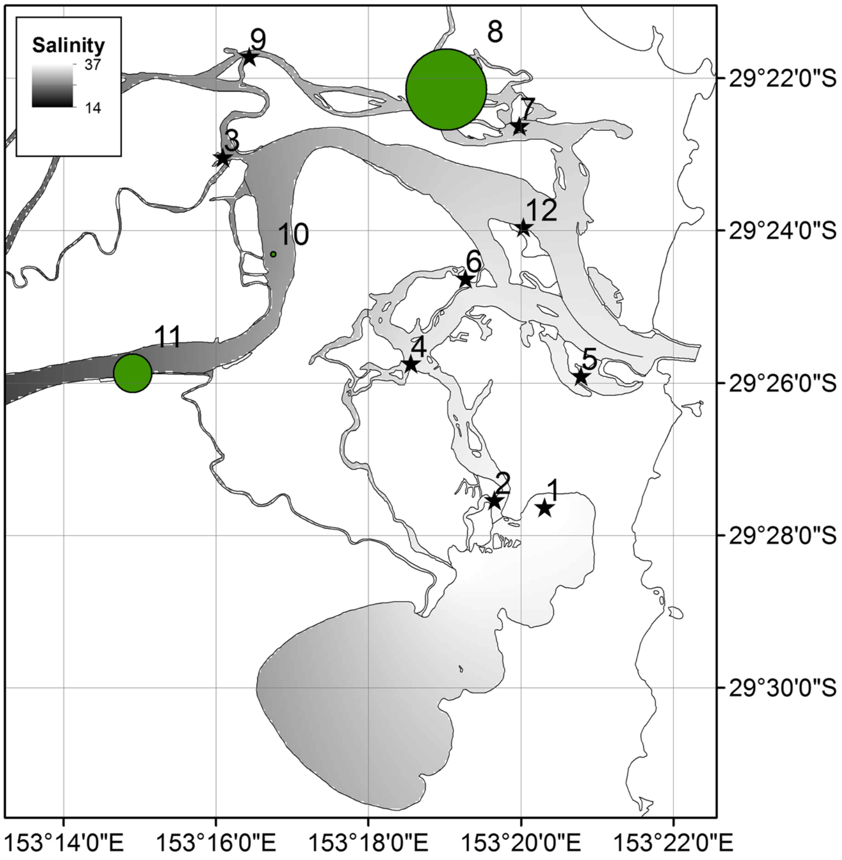

Fig. 3 Relative contribution of emigrating Eastern King Prawn among putative nursery habitat areas (actual contributions listed in Table 1), indicated by circle size. Areas that did not contribute shown as stars (note small contribution only from area 10). An interpolated salinity surface is shown (scale indicated in figure legend). Numbers correspond to Fig. 2 and Table 1

of greatest contribution (from the broad-scale assessment) or abundance (from the quantitative survey) occurring 8–12 km from the mouth. When considered alongside the trophic relationships described for Eastern King Prawn, these various lines of evidence suggest that nursery function of different areas within the lower estuary is a product of connectivity, recruitment and nutrition derived from primary productivity of vascular plants. The relationships observed have implications for the repair of habitats within the estuary, which have seen substantial degradation over decadal time scales (Fig. 7).

Table 1 Average isotopic composition (SE), $n = 3$, for 12 areas in Clarence River estuary and designation of effective juvenile habitat (bold) on the basis of contribution of sampled putative nursery habitat areas to Eastern King Prawn ($n = 68$) captured emigrating through mouth of estuary

Area	$\delta^{15}N$	$\delta^{13}C$	Contribution
1	8.08 (0.19)	−15.58 (0.36)	0.00
2	8.50 (0.14)	−16.04 (0.19)	0.00
3	8.07 (0.09)	−14.53 (0.09)	0.00
4	9.66 (0.18)	−14.86 (0.04)	0.00
5	8.58 (0.14)	−12.20 (0.05)	0.00
6	8.54 (0.06)	−13.15 (0.11)	0.00
7	8.93 (0.33)	−13.95 (0.23)	0.00
8	9.17 (0.35)	−16.83 (0.10)	**0.65**
9	9.99 (0.25)	−16.24 (0.17)	0.00
10	9.49 (0.12)	−16.49 (0.04)	0.04
11	9.34 (0.05)	−18.95 (0.14)	**0.31**
12	8.93 (0.07)	−15.82 (0.13)	0.00
Mean			0.08

Patterns in Effective Juvenile Habitat and Abundance of Eastern King Prawn

The broad-scale assessment indicated that the majority of the Eastern King Prawn emigrating from the estuary originated from the network of subtidal channels and deltaic islands within the North Arm of the lower estuary. This habitat is primarily shallow, unvegetated, subtidal soft sediment with limited seagrass cover but is surrounded by extensive intertidal mangrove and saltmarsh habitat. Similar habitats are also present in the network of deltaic islands connecting Lake Wooloweyah to Main Channel; however, these areas did not appear to contribute to the emigrating prawns. These findings were somewhat confirmed by the quantitative sampling program which found few Eastern King Prawns inhabiting this area. Quantitative sampling indicated the greatest abundance of prawns in 2015/16 was in Main Channel and also in North Arm 8–12 km from the estuary mouth.

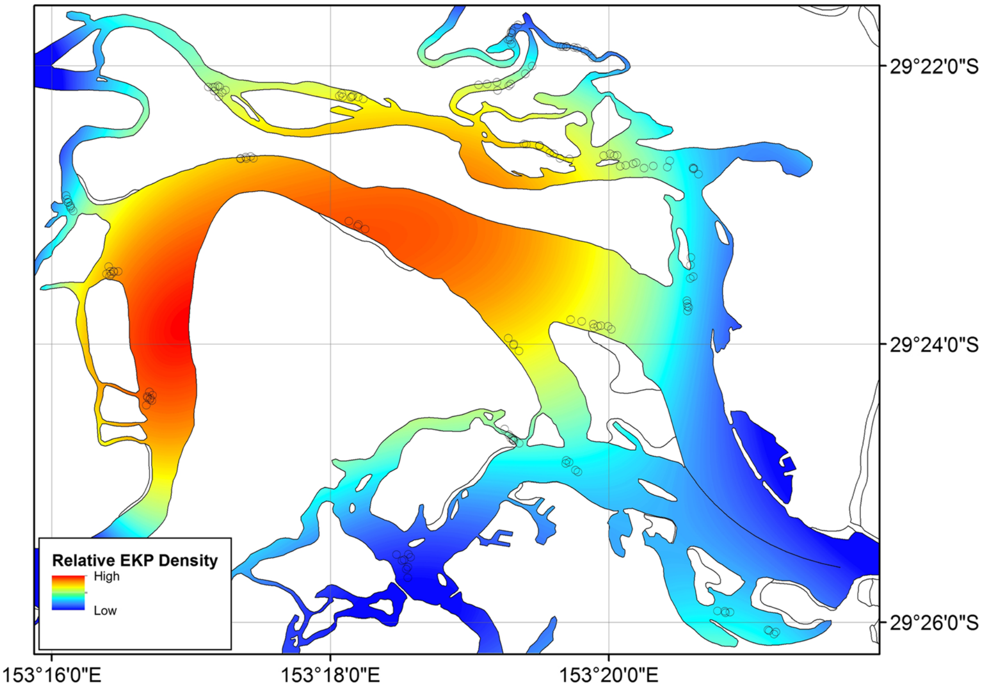

Fig. 4 Heat map showing global polynomial interpolation of relative Eastern King Prawn abundance across lower Clarence River estuary from quantitative sampling (scale indicated in figure legend). Unfilled circles indicate locations sampled (tows). The rock wall directing tidal flow toward main channel and North Arm is evident just inside estuary mouth

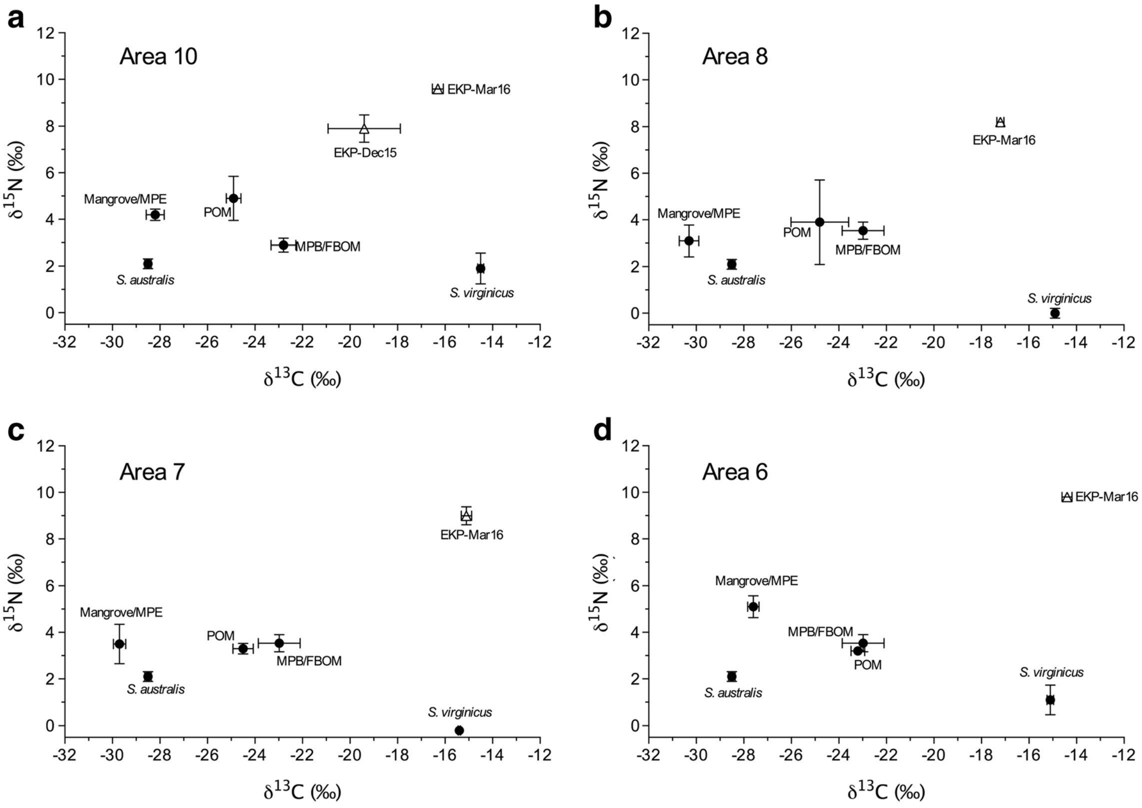

Fig. 5 Carbon and nitrogen stable isotope ratios for Eastern King Prawn (EKP; open triangles) and potential basal sources (closed circles) across lower Clarence River estuary for **a** area 10 ($n = 19$), **b** area 8 ($n = 16$), **c** area 7 ($n = 7$) and **d** area 6 ($n = 16$) (mean ± SE; area names correspond to Table 1 and Fig. 3). Mangrove/MPE, mangrove leaves and mangrove pneumatophore epiphyte; MPB/FBOM, microphytobenthos and fine benthic organic matter, POM, particulate organic matter; *S. virginicus*, *Sporobolus virginicus*; *S. australis*, *Suaeda australis*. EKP caught in December 2015 and March 2016 are shown for area 10 (panel **a**)

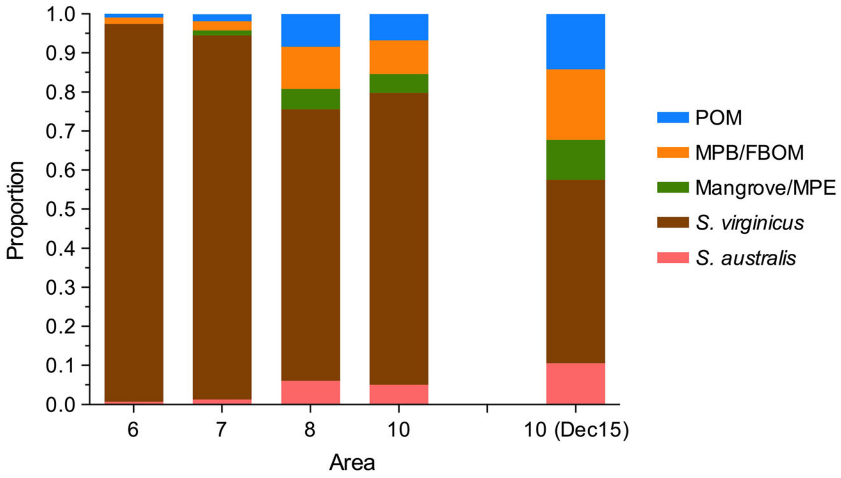

Fig. 6 Mean feasible contributions of five potential food sources for Eastern King Prawn (EKP) at areas 6, 7, 8 and 10 sampled in March 2016 (and area 10 December 2015). Area names correspond to Table 1, Fig. 3 and Fig. 5. Proportions calculated after correction for ^{13}C trophic level fractionation (described in the text). Only ^{13}C values were included in IsoSource modelling

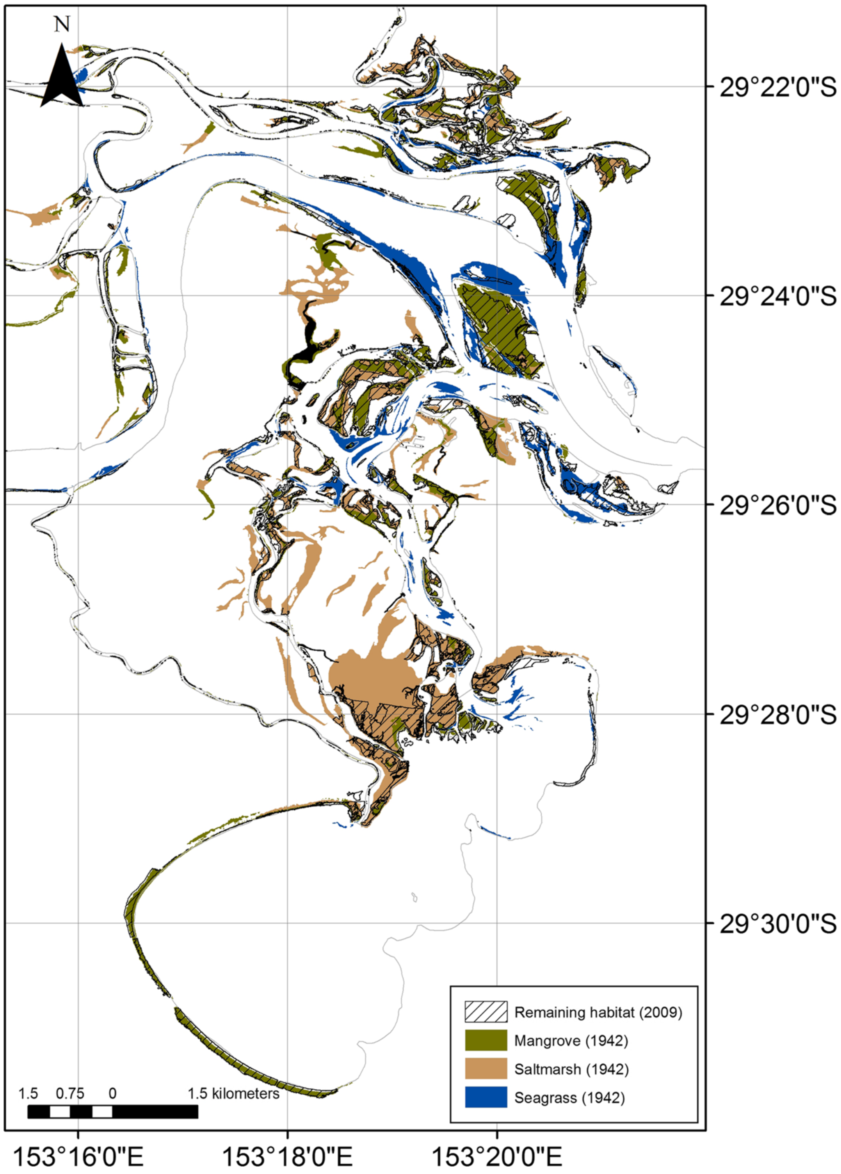

Fig. 7 Extent of habitat loss in lower Clarence River estuary between 1942 and 2009. Figure legend indicates main habitat classes present in 1942. Areal extent of habitat classes in 2009 indicated with overlaid diagonal hatching. Historic (1942) and current habitat data obtained from NSW Department of Primary Industries–Fisheries, Habitat Mapping Database (courtesy of G. West)

The observed patterns in abundance and contribution to the adult stock in our study are not so surprising when the morphology of the estuary is taken into account. Recent studies highlight the effect of circulation and connectivity on recruitment of penaeid prawns, as well as the designation of Nursery Habitat or Effective Juvenile Habitat for these species. In a study of the Laguna Madre estuary in Mexico, Blanco-Martínez and Pérez-Castañeda (2017) found that *Farfantepenaeus* spp. were most abundant in seagrass beds near the estuary mouth. Taylor et al. (2017) explored distribution patterns for Eastern King Prawn in Lake Macquarie, another wave-dominated estuary in south-eastern Australia, and found that abundance peaked in seagrass beds at intermediate distances from the estuary mouth, due to a combination of both tidal forcing and wind-driven circulation.

In the Clarence River, a rock wall forms a prominent feature of the morphology of the estuary mouth, ultimately directing the bulk of tidal flow up Main Channel and toward North Arm. This may affect the ability of ocean-spawned Eastern King Prawn postlarvae to recruit into the south arm of the estuary and Lake Wooloweyah, providing one explanation for the low abundance of Eastern King Prawn in this area and the lack of any detectable contribution of this part of the estuary to the adult population. Consequently, despite there being abundant macrophyte habitat and appropriate salinity to support juvenile Eastern King Prawn, limited connectivity may contribute to recruitment limitation for this species in the southern part of the lower estuary.

Contribution of Basal Sources of Nutrition to Eastern King Prawn

At the time of sampling, the dominant sources of carbon had reasonably similar isotope values in each area and these values were similar to those reported elsewhere in Australia for saltmarsh, mangrove and MPB (Melville and Connolly 2003; Melville and Connolly 2005; Abrantes and Sheaves 2008; Mazumder and Saintilan 2010; Connolly and Waltham 2015). The saltmarsh grass, *S. virginicus*, was the dominant nutritional source for Eastern King Prawn in all areas, ranging from 47 to 97%. Eastern King Prawn have a varied diet, typically comprised of plant material, detritus, crustaceans, microorganisms, small shellfish and worms (Racek 1959; Moriarty 1977; Suthers 1984). Carbon fixed by saltmarsh vegetation makes an important contribution to the nutrition of other penaeids (Abrantes and Sheaves 2008) and other invertebrates (Guest and Connolly 2004). If a buffer of radius 750 m (chosen to avoid overlap between adjoining sites) is placed around sampling areas, *S. virginicus* represents a maximum of 35% of the vegetated area. In contrast, mangrove habitat represents up to 100% of the available vegetated habitat, but mangroves only support a maximum of 8% of Eastern King Prawn diet. Throughout the entire Clarence River estuary, saltmarsh represents 26% of the vegetated habitat, whereas mangroves represent 67%.

The movement of carbon within an estuary can range from a few meters (Guest and Connolly 2004) to adjacent habitats (Connolly et al. 2005; Melville and Connolly 2005) and even kilometres (Gaston et al. 2006). As a consequence, organisms do not always derive nutrition from primary production in their immediate area and can be supported by other sources. In subtropical Australia (Moreton Bay), shorecrabs (*Parasesarma erythrodactyla* and *Australoplax tridentata*) in mangroves have stable isotope signatures that reflect incorporation of saltmarsh grass and microphytobenthos but not mangrove material (Guest and Connolly 2004; Guest et al. 2006). Similarly, in a tropical Australian estuary (Ross River), the Banana Prawn *Penaeus merguiensis* has relatively high δ^{13}C values consistent with the incorporation of *S. virginicus*, even in areas with extensive mangrove habitat (Abrantes and Sheaves 2008). While transport of organic matter throughout estuaries is clearly important, the apparent contribution of saltmarsh grass to estuarine food webs can sometimes be uncertain, as it shares a similar isotope value to seagrass (Melville and Connolly 2005). In the Clarence River estuary, there is a much greater areal extent of saltmarsh than seagrass, particularly in the areas that are important to Eastern King Prawn (see Figs. 1 and 7). In addition, recent work by Connolly and Waltham (2015) shows that the role of seagrass as a nutrient source for consumers declines exponentially over distances < 100 m from seagrass beds, indicating that any influence of seagrass would be highly localised. This was in contrast to saltmarsh grass, which showed no such decline with distance (Connolly and Waltham 2015). These factors provide further support for our conclusion that saltmarsh grass is the dominant nutritional source for Eastern King Prawn productivity in the Clarence River.

Our analysis also indicated that the importance of saltmarsh to Eastern King Prawn diet showed some temporal variation, with the mean proportion of *S. virginicus* increasing from 47% in December to 75% the following March for area 10. This may be explained by the environmental conditions influencing the estuary earlier in the season. Substantial (up to 45 ML day^{-1}) freshwater inflows to the Clarence River were observed from October to December 2015, whereas negligible inflow was observed from mid-January to April 2016 (NSW Office of Water Pineena Database, station 204055). The greater freshwater inflow in late 2015 potentially displaced the saltmarsh material accumulated in the estuary and replaced it with organic material (POM) from the upper catchment which has a more depleted δ^{13}C signature. This could explain the greater proportion of POM in the diet in December relative to March.

Interpretation of trophic relationships determined using IsoSource is not without limitations. The contribution of each basal resource to a particular consumer is usually not known exactly, because the number of major basal source pools may exceed the number of stable isotope ratios available for analysis (Layman 2007). In addition, IsoSource results do not actually correspond to an exact solution for the diet of a species, but to a distribution of possible solutions, given a set of possible basal sources (Abrantes and Sheaves 2008). In this study, the IsoSource results are reported with reasonable confidence because there is minimal variation in the isotopic composition of basal resources among sampling areas, and the 1st and 99th percentile were within a narrow range of the mean value. Furthermore, *S. virginicus* was the only likely basal resource with an enriched δ^{13}C value relative to Eastern King Prawn, and the isotopic difference between Eastern King Prawn and the major basal resource was similar among sampling areas.

Management Implications

The Clarence River is the largest estuarine system in New South Wales and supports the state's largest estuarine commercial fishery. The lower catchment is dominated by agriculture (primarily cane farming), and the installation of flood gates and historic reclamation for agriculture and development has led to substantial habitat loss. Comparison between the areal extent of habitat in 1942 and 2009 (calculated from the NSW Department of Primary Industries–Fisheries, Habitat Mapping Database) indicates that 63% of saltmarsh habitat (512 ha) and 79% of seagrass habitat (316 ha) have been lost, with most of this loss concentrated in the lower estuary (Fig. 7). Conversely, areal coverage of mangrove habitat has increased by ~ 6% during this time. In addition, > 60 ha of waterway area has been lost during this period.

The data presented here indicate that saltmarsh is an important habitat supporting productivity of juvenile Eastern King Prawn within the estuary. Much of the lost saltmarsh habitat is around the mouth of Lake Wooloweyah, where high numbers of Eastern King Prawn recruits are unlikely to occur. However, outwelling of saltmarsh material from this area to other areas of the estuary is likely, so the impacts of this loss may be relevant across the estuary. Also, substantial losses of saltmarsh habitat have also occurred along Main Channel in the lower estuary, and it is likely that the loss of this habitat has had consequences for the productivity of Eastern King Prawn, as well as other species that feed in food webs supported by saltmarsh productivity.

While we have demonstrated the importance of saltmarsh to Eastern King Prawn in terms of direct occupation and trophic subsidy, we did not directly address the benefits different estuarine habitats provide as a refuge from predation. Evidence from other systems highlight the dual role provided by these habitats (i.e. food and refuge, Boesch and Turner 1984); however, recent work suggests direct occupation of these habitats may not be as prevalent for commercial species as previously thought (Becker and Taylor 2017; Sheaves 2017). Eastern King Prawn certainly occur in subtidal channels draining saltmarsh, but there is a lack of data on the use of these habitats by predatory species in south-eastern Australia to evaluate whether these habitats offer a reduced risk of predation. At this stage, additional benefits of saltmarsh and mangrove habitats as refugia remain a possibility and a topic for future research.

Repair of estuarine habitat through the reinstatement of tidal flow is a potential management action which would both re-establish key estuarine habitat and most probably support increased productivity of nektonic species (Boys et al. 2012; Boys and Williams 2012). For example, in the Hunter River, the removal of culverts and the return of tidal flow to a series of creeks which fed a complex intertidal wetland system resulted in immediate changes to the fish and crustacean communities, whereby they began to reflect communities in unimpacted reference locations (Boys and Williams 2012). Furthermore, research in the Clarence River itself has showed that floodgate remediation enhanced the passage and connectivity of crustaceans and fish, including exploited species (Boys et al. 2012). These examples highlight how management actions such as reinstatement of connectivity within the estuary can result in beneficial ecological outcomes for commercially important species. As wetland systems recover, it is likely that they will also provide a trophic subsidy to other areas of the estuary.

Conclusions

Stable isotope ratios have routinely been used to determine the relative importance of mangrove material to the estuarine food web (Melville and Connolly 2003; Melville and Connolly 2005; Layman 2007; Abrantes and Sheaves 2008). Here, we show the importance of saltmarsh-derived material in providing nutritional support for juveniles of a commercially important penaeid species. Fry and Ewel (2003) suggest that a broader focus that examines patterns in habitat usage alongside trophic relationships resolved through isotopic composition contributes to a clearer evaluation of the importance of habitat for exploited species. The combination of connectivity modelling (based on isotope data), quantitative sampling and food web analysis employed here has provided a holistic snapshot of nursery habitat function within the lower Clarence River estuary. There is a clear link between Eastern King Prawn and saltmarsh habitat, both in the direct occupation of subtidal channels by juvenile prawns, and also in support of productivity from saltmarsh-synthesised primary production. This demonstrates the importance of these habitats for Eastern King Prawn, and it is likely that other exploited species in these habitats are similarly supported by marsh-derived productivity. These findings indicate that repair of the extensive habitats lost to the system are likely to yield significant benefits for Eastern King Prawn. Our appreciation of the importance of saltmarsh in the lower reaches of estuarine systems, and the potential outcomes from habitat repair will be further improved by examining these relationships for other species.

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