Changes in the abundance of the Western School Prawn (2013-2018) in association with a restocking program

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Photographs: (Cover) Murdoch researchers setting the otter trawl for a trial sampling run in the Swan-Canning Estuary. (This page; top left to bottom right) The former Western Australian Minister for Fisheries, the Hon. Ken Baston, releasing juvenile Western School Prawns; Will Smithwick prawning; Kevin Reid and his family with a catch of prawns. Photos taken by Stewart Allen.

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Acknowledgements

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Executive summary

The Western School Prawn *Metapenaeus dalli* (an estuarine species in south-western Australia) and the Western King Prawn *Penaeus latisulcatus* (a marine species) were the focus of a small commercial and iconic recreational fishery in the Swan-Canning Estuary. However, the commercial fishery closed in the mid-1970s and recreational fishing participation also declined from the 1990s, with the last significant catches of *M. dalli* recorded in the late 1990s. The reasons for the decline in *M. dalli* are unclear and, despite a large reduction in fishing pressure, stocks of this penaeid had not recovered by 2007. Therefore, restocking was seen as a possible means of increasing the population size of *M. dalli* in the estuary.

Restocking was undertaken over four years between 2012/13 and 2015/16 and involved the release of ~4.65 million post-larval *M. dalli*. The abundance, size and reproductive status of male and female *M. dalli* and *P. latisulcatus* were recorded at 20 sites in the shallow, nearshore waters (from hand trawls) and 16 sites in the deeper, offshore waters of the Swan-Canning Estuary (from otter trawls), every lunar month between October and March (the breeding season) over five years between October 2013 and March 2018. The resultant data, derived from 1,240 hand trawls and 962 otter trawls, were used to determine whether the density and population fecundity of *M. dalli* changed over those five years and if *P. latisulcatus* showed similar patterns of change in abundance to *M. dalli*.

Densities of *M. dalli* increased sequentially from 2013/14 to 2015/16, in both nearshore waters, where individuals migrate to spawn, and offshore waters. In this later year densities had increased by 58 and 109% in nearshore and offshore waters, respectively, compared to those at the start of the study (2013/14) and after the release of only ~1,000 post-larvae. However, the extent to which the restocking contributed to the increased abundance of *M. dalli* is not definitively known, as the hatchery-reared individuals were unable to be marked to distinguish them from wild-spawned stock. The increased abundance and/or size of *M. dalli* led to successive increases in egg production in both water depths between 2013/14 and 2015/16 with the combined value for 2015/16 being twice that of the previous year and over three times greater than that in 2013/14.

Given the relatively large size of the *M. dalli* population and egg production in 2015/16 it was surprising that densities in both water depths in 2016/17 decreased by > 90% and egg production by 85% compared to 2013/14. This may reflect hypoxic events that occurred between April and June 2016 in the Middle Swan Estuary, a key habitat at that time of year, areas and the atypically low air and water temperatures that occurred during winter of 2016 and extended into spring. *Metapenaeus dalli* is a subtropical species, sensitive to hypoxia and whose population in the Swan-Canning Estuary is almost at the poleward limits of its range. Thus, in south-western Australia, it is confined to estuaries rather than the coastal waters due to the relative warmth they provide. These cooler waters could have resulted in direct mortality, but would also have reduced the period of the year when individuals could grow to reduce their susceptibility to predation, resulting in increased levels of indirect mortality. This overwintering mortality is known to similarly affect populations of portunid crabs towards the limit of their spatial range. The cooler temperatures and slower growth also delay the onset of maturity in *M. dalli*.

The lower abundances, delayed maturity and typically smaller size of *M. dalli* reduced egg production at the start of the 2016/17 breeding season. Moreover, in February 2017, when some of those individuals would have attained sexual maturity and spawned, an aseasonal rainfall event occurred, leading to marked increases in freshwater discharge, water column stratification and hypoxia. This was mainly seen in the Lower Canning Estuary and Melville Water, which, at this time of year, harbour large numbers of *M. dalli* in both water depths. Following this event, very low numbers of *M. dalli* were caught in the remaining two months of the breeding season and none were gravid (*i.e.* egg production = zero). Even fewer *M. dalli* were collected in 2017/18; only 4 and 3% of the 2013/14 population in the nearshore and offshore waters, respectively. By contrast, numbers of *P. latisulcatus* remained relatively consistent over the five years of the study, and even increased significantly in abundance in the nearshore waters in 2017/18 compared with 2013/14.

In summary, the dramatic changes in the abundance of *M. dalli* over the five years was most likely caused by the releases of hatchery-reared post-larval prawns and the persistence of marine-like salinities and predominantly normoxic conditions in the first three years (2013/14-

2015/16) providing positive influences on density. These were then followed by a series of hypoxic events (April-June 2016) and a cooler than average overwintering period in 2016, which extended into spring. These negative influences culminated in an aseasonal rainfall event causing widespread hypoxia during the breeding season of 2016/17. The spatial extent of this hypoxia affected the primary area of the estuary most utilised by *M. dalli.* These events have resulted in the current abundance of *M. dalli* being very low in 2017/18, even compared to pre-restocking levels. This species is particularly vulnerable to changing conditions in the estuary, as it spends its entire life within the Swan-Canning and is thus unable to recruit from outside populations. Moreover, crustaceans are typically sensitive to low levels of oxygen, and are less mobile than other taxa, (*e.g.* pelagic teleosts) and thus less able to readily escape relatively large areas of hypoxia.

The current abundance of *M. dalli* is very low, to the point where collecting enough broodstock for another restocking project may be difficult and thus very expensive. Given the iconic nature of this species, there is value in monitoring the population in the future in association with management of the fishery, but not until several breeding seasons have passed, and no aseasonal summer rainfall events have occurred.

Introduction

Aquaculture-based enhancement (ABE), which encompasses restocking, stock enhancement and sea ranching, provides a mechanism to supplement fishery resources and restore, maintain and increase productivity (Lorenzen *et al.*, 2013; Taylor *et al.*, 2017a). If implemented successfully, such enhancement can support systems recovering from anthropogenic perturbations, such as over-exploitation and habitat degradation, increase food security and augment economic and social values (Bell *et al.*, 2005; Kitada and Kishino, 2006; Arlinghaus *et al.*, 2014). These programs are often popular with recreational fishers, as they are seen as ways of increasing the availability of fish without placing input, output and/or access controls on the fishery, and align with the fishers' preference for a higher abundance of fish, larger size of fish and a greater chance of a catch (Arlinghaus and Mehner, 2005; Garlock and Lorenzen, 2017; Obregón *et al.*, in press).

Despite the attraction of such programs, the performance of many has been mixed and, more often than not, disappointing (Bell *et al.*, 2005; Lorenzen, 2005). Indeed, many have failed to significantly increase fishery production, provide economic benefits and/or have had detrimental effects on the natural population of the targeted species (Hilborn, 1998; Levin *et al.*, 2001; Kitada *et al.*, 2009; Kitada, 2018). Thus, there has been a major effort to improve the way release programs are developed, implemented and assessed, resulting in the development of the responsible approach to stock enhancement (Blankenship and Leber, 1995; Lorenzen et al., 2010). The revised responsible approach is a set of 15 principles representing three stages; i) initial appraisal and goal setting; ii) research and technology development and iii) operational implementation and adaptive management, considered essential to control and optimise enhancement (Lorenzen et al., 2010).

Typically, ABEs have occurred mainly in freshwater or marine/coastal environments (Welcomme and Bartley, 1998; Bartley *et al.*, 2015; Ingram and De Silva, 2015). For example, more than 160 freshwater species are farmed commercially and available for enhancement. Ingram and De Silva (2015) and Lorenzen *et al.* (2000) estimated that the culture-based fisheries for freshwater and diadromous organisms contributed 2 million mt per year, accounting for about 20% of recorded freshwater capture yields. Moreover, approximately 180 different species have been released into marine and coastal environments in a total of 64 countries worldwide (Born *et al.*, 2004). This global trend also applies to Australia, where ABE has been used to primarily benefit freshwater and marine fisheries, in particular, for salmonids (Blount *et al.*, 2017; Partridge *et al.*, 2017), with few releases undertaken in estuaries (Loneragan *et al.*, 2013). Despite this, Taylor *et al.* (2005) argued that due to the lack of any substantial upwelling in coastal Australia waters and the demonstrated lack of success in stocking oceanic species, ABE releases in Australia should be confined to estuaries, and on species that are obligate users of the estuary and are recruitment limited. Further justification of this is provided by Creighton *et al.* (2015) who estimated that, in Australia, estuarine species comprise > 75% of the commercial fish catch in coastal waters and, in some regions, up to 90% of the recreational angling catch.

A number of biological characteristics make a species suitable for ABE (Garlock *et al.*, 2017), including fast growth rate and high site fidelity. Due to the high productivity in estuaries, which, in turn, provides large quantities of food, coupled with the typically reduced presence of large predator species (Tweedley *et al.*, 2016b), fish have been shown to grow faster and suffer lower natural mortality in estuarine than adjacent coastal waters (Potter *et al.*, 2011). Moreover, the stocking of species that complete their life cycle in estuaries ensures that they remain within the systems, and are ‘available’ for reproduction and harvest (Cottingham *et al.*, 2015). However, while the provision of nutrients through allochthonous inputs can increase primary productivity, excess nutrients can lead to a range of deleterious effects, such as algal blooms and hypoxia (Davis and Koop, 2006; Anderson *et al.*, 2008a; Zhang *et al.*, 2010). The effects of such anthropogenic perturbations are amplified in microtidal estuaries in Mediterranean climates, such as those in south-western Australia, due to their long water residence times and highly seasonal rainfall (Tweedley *et al.*, 2014; Warwick *et al.*, 2018). Moreover, extreme climatic events, such as aseasonal rainfall from cyclones, *e.g.* significant rainfall in the typically dry summer months, can influence the physico-chemical environment of microtidal estuaries, which, in turn, alter the composition of faunal communities (Tweedley *et al.*, 2016a; Hoeksema *et al.*, 2018).

While crustaceans are particularly sensitive to the impacts of natural and anthropogenic perturbations (Warwick and Clarke, 1993; Wu *et al.*, 2002; Tweedley *et al.*, 2016a), species such as crabs and penaeid prawns are often targeted by commercial and recreational fishers. The genus *Metapenaeus* is one of 25 extant genera belonging to the Penaeidae, and comprises 29 species that occur exclusively throughout the inshore coastal and estuarine waters of the Indo-West Pacific (De Grave, 2014). In this region, species of *Metapenaeus* contribute to important commercial and recreational fisheries and aquaculture production (Dichmont *et al.*, 2006; Kompas *et al.*, 2010). For example, in subtropical and temperate New South Wales, an average of 1,410 tonnes of prawns, valued at more than AUD $18 million, were caught annually between 2004 to 2009 in inshore and estuarine environments, with *Metapenaeus macleayi* and *Metapenaeus bennettae* comprising 54% and 32% of the total catch by weight and value, respectively (Montgomery, 2010). Prawns found in estuaries in this region, mainly *Penaeus* (=*Melicertus*) *plebejus* and *M. macleayi*, are also exploited by recreational fishers who remove ~4,700 tonnes annually (Montgomery, 2010).

Metapenaeus dalli, the Western School Prawn, is the only metapenaeid found in temperate south-western Australia (Racek, 1957). This species typically occurs in shallow, inshore marine waters (< 30 m deep) along the western coast of Australia from Darwin in the north to Cape Naturaliste in the south and also occur in Java, Indonesia (Grey *et al.*, 1983; Fig. 1). However, in latitudes below 31º S, it is only found in estuaries (Potter et al., 1986; Potter et al., 1989) and is believed to complete its entire life cycle within these systems (Broadley *et al.*, 2017; Crisp *et al.*, 2017b; 2018b). It is thus classified as a solely estuarine species in this region (Potter *et al.*, 2015a; 2015b; Fig. 2), whereas the co-occurring Western King Prawn *Penaeus* (= *Melicertus*) *latisulcatus* (Poh et al., 2019), a species that spawns in the marine environment, whose juveniles spend significant time in estuaries, is classified as a marine estuarine-opportunist (Fig. 1; Penn, 1980).

Both *M. dalli* and *P. latisulcatus* were the focus of a small commercial and iconic recreational fishery in the Swan-Canning Estuary. The commercial fishery catch peaked at 15 tonnes in 1959, but declined afterwards leading to its closure in the mid-1970s (Smith, 2006). At its peak, recreational prawning in this estuary involved over 50,000 people and became an iconic pastime, particularly during the Christmas period (Smithwick *et al.*, 2011). However, recreational catch rates also declined, with the last significant catches recorded in the late 1990s (Maher, 2002). This decline is thought to be due to a combination of overfishing, changing environmental conditions and recruitment failure (Smith, 2006; Smith *et al.*, 2007). Despite the large reduction in fishing pressure, *M. dalli* populations had not recovered and thus a restocking program was initiated (Tweedley et al., 2017b).

Following the principles of responsible aquaculture-based enhancement (Lorenzen et al., 2010) approaches, this restocking was accompanied by a research and development program that i) developed new aquaculture techniques (Crisp et al., 2016; 2017c; Jenkins et al., 2017; Crisp et al., 2018a), ii) determined the growth, mortality and reproduction of *M. dalli* (Broadley *et al.*, 2017; Crisp *et al.*, 2018b; Fig. 2), iii) investigated the ecology of *M. dalli* and co-occurring species to better understand factors affecting their natural recruitment and to develop a sound a release strategy (Tweedley et al., 2017a; Poh et al., 2018) and iv) established a monitoring program to track the changes in abundance of *M. dalli* over time to help evaluate the success of the restocking. The aims of the current study were to i) document any changes in abundance and population fecundity of *M. dalli* in the nearshore and offshore waters of the Swan-Canning Estuary in the five years since the start of the restocking program and ii) compare the trends in abundance *M. dalli* to those of the co-occurring *P. latisulcatus*.

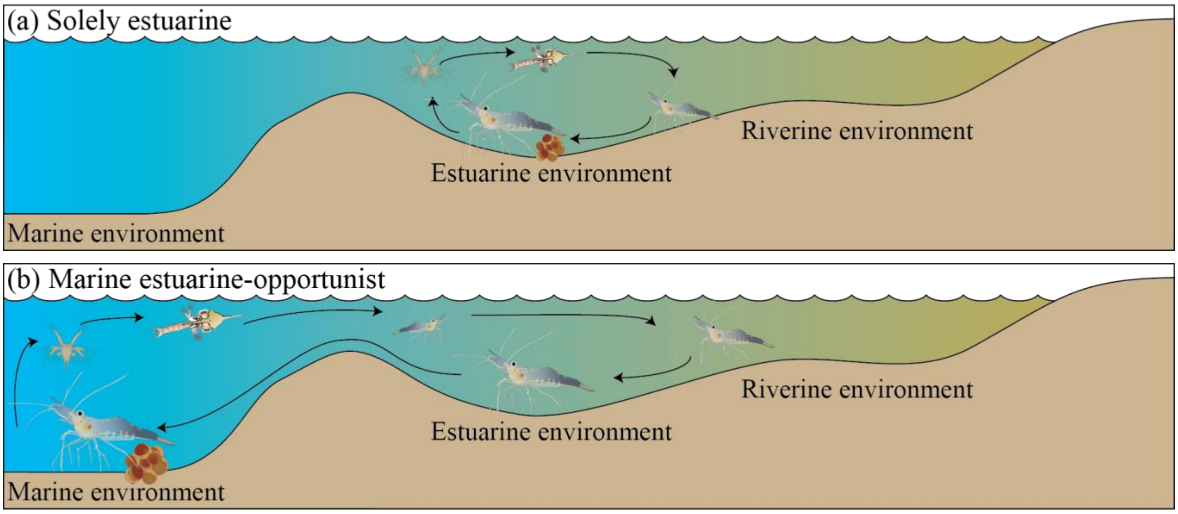

Fig. 1. Conceptual models of the life cycle of the (a) solely estuarine Western School Prawn *Metapenaeus dalli* and (b) the marine estuarine-opportunist Western King Prawn *Penaeus latisulcatus* in the Swan-Canning Estuary. Note that north of 31 °S, *M. dalli* is found in coastal marine embayments. Modified from Potter *et al.* (2015b).

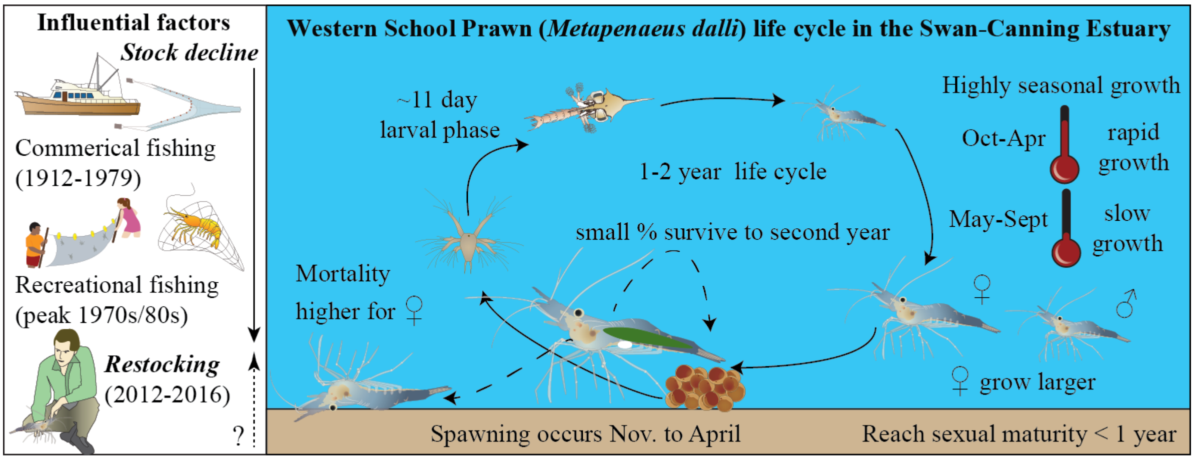

Fig. 2. Conceptual models of the life-history characteristics of *Metapenaeus dalli* in the Swan-Canning Estuary. Adapted from Broadley *et al.* (2017).

Materials and methods

Study site

The Swan-Canning Estuary is a drowned river valley system located in south-western Australia, which is ~50 km long, covers an area of ~55 km^2 and remains permanently-open to the Indian Ocean (Brearley, 2005). The estuary comprises a narrow entrance channel that opens into two basins (Melville and Perth Water) and the tidal portions of the Swan and Canning Rivers, which extend ~29 and 13 km upstream from their entry points into Melville Water, respectively. Although the majority of the estuary is shallow, *i.e.* < 2 m in depth, it reaches a maximum depth of ~20 m in the entrance channel. South-western Australia experiences a Mediterranean climate, with hot, dry summers and cool, wet winters with ~80% of rainfall occurring between June and September (Gentilli, 1971; Hodgkin and Hesp, 1998; Hallett *et al.*, 2018). This, combined with the microtidal tidal regime (< 2 m variation in tide height), results in marked seasonal variations in water physical-chemical conditions in this salt-wedge estuary. Salinities are typically stable and relatively high throughout much of the estuary during the austral summer (December to February), but during winter, may vary markedly along the estuary following substantial freshwater discharge, leading to pronounced stratification of the water column and hypoxia (Tweedley *et al.*, 2016a; 2016b).

The estuary flows through the capital city of Perth, which supports ~78% of the 2.6 million people in the state of Western Australia (Australian Bureau of Statistics, 2015). It is highly valued for its aesthetic, commercial, environmental and cultural importance (Malseed and Sumner, 2001). Recreational fishing is an iconic activity in WA, with an estimated 711,000 participants in 2014/15 (Ryan *et al.*, 2015), and the Swan-Canning Estuary is a popular hotspot for recreational fishers, with an estimated effort of 30,338 fisher days occurring in 1998/99 (Malseed and Sumner, 2001).

Sampling regime

Prawns were sampled at two locations within 20 nearshore (< 2 m deep) and 16 offshore sites (2-17 m deep) in the Swan-Canning Estuary at night between ~18:00 and 01:00, on every new moon phase (moon <10% illumination), between October and March (*i.e.* the breeding season;

Broadley *et al.*, 2017) in each of five years between 2013/14 and 2017/18 (Fig. 3). During the course of this study, ~4.65 million post-larval *M. dalli* were released during the austral summer and autumn between December 2012 and March 2016. The number released increased sequentially among years with ~1,000 released in 2012/13, ~635,000 in 2013/14 and ~2,000,000 in both 2014/15 and 2015/16 (Jenkins *et al.*, 2017; Tweedley *et al.*, 2017). Thus the first four years of data follow releases of post-larval *M. dalli* in the previous year, whereas no releases were carried out in the year before the final sampling in 2017/18 (Fig. 4).

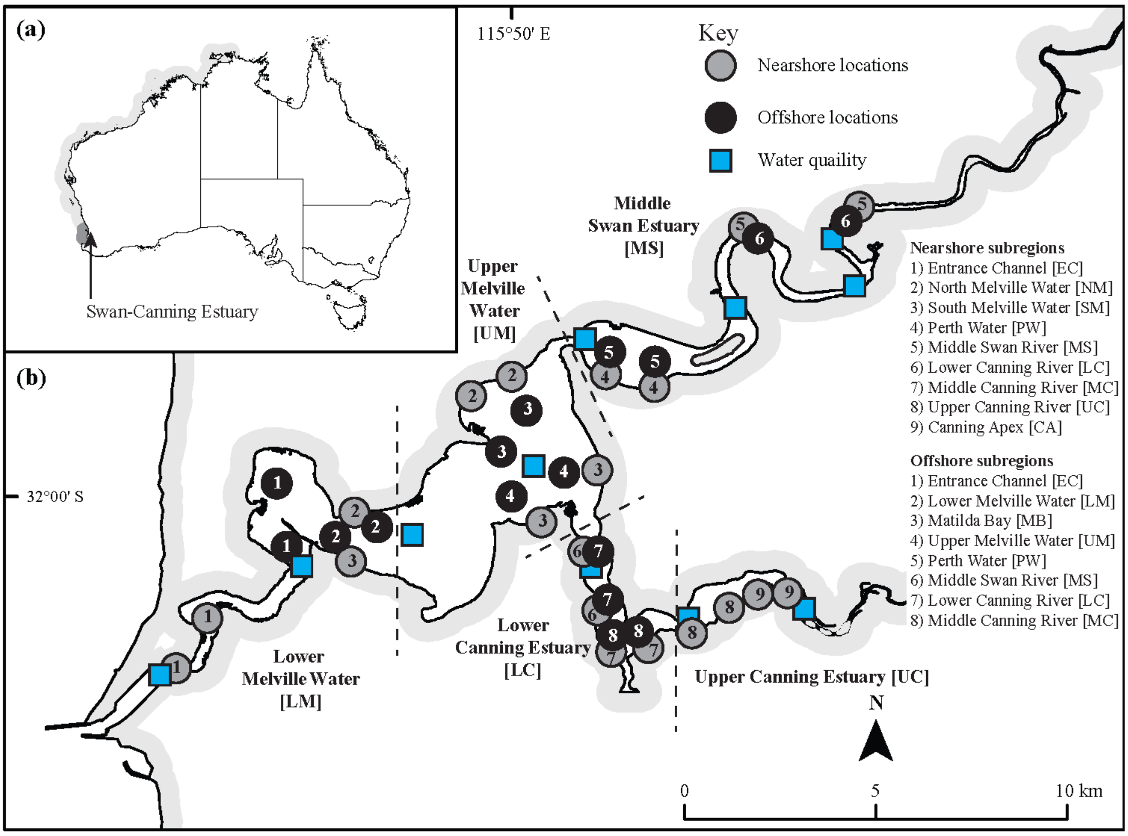

Fig. 3. Map showing (a) Australia and the distribution of *Metapenaeus dalli* in inshore marine waters (light grey) and solely in estuaries (dark grey) and (b) 20 nearshore (●) and 16 offshore (●) sites in Swan-Canning Estuary sampled in each month between October and March in the five years between 2013/14 and 2017/18. Dotted lines denote the separation among the five broad regions (bold face) of the estuary. Codes for regions and subregions are given in square brackets. ■ denotes the sites at which weekly water quality measurement were taken by the Department of Water and Environmental Regulation for the Department of Biodiversity, Conservation and Attractions.

Sites were spread from close to the mouth of the estuary (~2.5 km) to 34 and 27 km upstream in the Swan and Canning rivers, respectively. Sites were categorized into five broad regions in nearshore waters (which comprised nine subregions) and four broad regions in the offshore waters (comprised of eight subregions), respectively (Fig. 3). Nearshore sites were sampled using a 4 m wide hand trawl constructed from 9 mm mesh. The width of the hand trawl net during trawling was, on average, ~2.85 m, but varied slightly amongst trawls depending on the condition of the substratum, presence of submerged obstacles and localised wind and wave conditions. Each hand trawl was 200 m in length and swept an area of ~570 m^2 and, on any single lunar cycle, covered a total area of 22,800 m^2.

Offshore waters were sampled using a small otter trawl that was 2.6 m wide and constructed of 25 mm mesh in the body and 9 mm mesh in the cod-end. The net was towed at an average speed of 1.6 knots (~3 km h^{-1}) for 5 min, covering a distance of ~250 m (swept area ~650 m^2) on each sampling period, covering a total area of 20,800 m^2. Note that due to a boat engine malfunction in December 2014, catch data were not obtained from all offshore sites and thus data from this month were removed from all analyses.

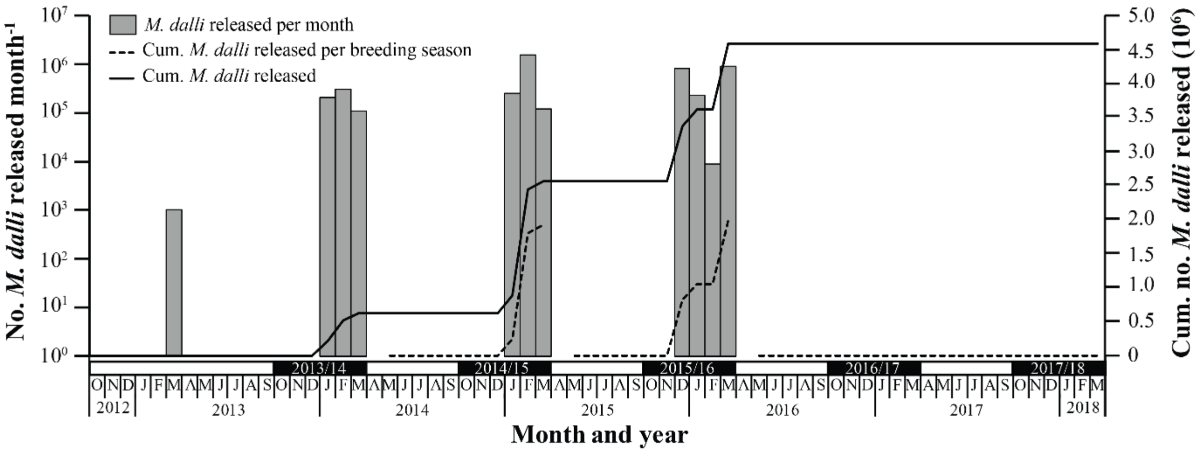

Fig. 4. Timeline showing the timing and magnitude of the release of post-larval *Metapenaeus dalli*, including the cumulative number of *M. dalli* released during each breeding season (October to March) and the duration of the restocking project. Months where monitoring of the prawn populations was undertaken are shaded in black. No *M. dalli* released after March 2016.

Prawns caught from October 2013 to December 2014 were euthanized in an ice slurry and transported to the laboratory for measurement (see below), except when a large trawl catch was made. A portion of these large catches was retained and the remainder of the catch returned to the water alive, with counts then scaled up accordingly. From January 2015 to March 2018, all retained prawns were counted, sized, sexed and presence or absence of a spermatophore identified (in females), before being returned to the water alive.

For prawns that were retained in the laboratory, the carapace length (CL), *i.e.* the distance from the post-orbital margin to the dorso-posterior point of the carapace (± 0.01 mm) and wet weight (± 0.01 g) were measured and their sex recorded in the laboratory. A subset of individuals was also measured for total length, with measurements taken from the anterior tip of the rostrum to the posterior tip of the telson, and wet weight (n = 797). Females and males were distinguished by the presence of a thelycum and petasma, respectively. The presence or absence of a spermatophore on females was recorded. Gravid *M. dalli*, with ovaries showing macroscopic signs of being at the late maturing or mature stages, as described by Crisp *et al.* (2017b), were recorded.

Water temperature, salinity, and dissolved oxygen concentration were measured at 50 cm intervals throughout the entire water column on a weekly basis at eleven sites throughout the area where sampling for prawns was undertaken (by Department of Water and Environmental Regulation [DWER] for the Department of Biodiversity, Conservation and Attractions [DBCA], Western Australia; Fig. 3). Thus, these data were measured regardless of whether prawns were collected. Data from April 2013 to March 2018 were extracted from an online database (http://wir.water.wa.gov.au/Pages/Water-Information-Reporting.aspx) and the water temperature, salinity and dissolved oxygen concentration in the surface and bottom 1 m of the water column at each site in each week were averaged. Daily records of rainfall and average minimum and maximum air temperature for Perth airport were obtained from the Bureau of Meteorology (http://www.bom.gov.au/climate/data/) between April 2013 and March 2018.

Statistical analyses

A data matrix containing the daily value for rainfall and average minimum and maximum air temperature was used to construct a separate Euclidean distance matrix for each climatic variable. Each matrix was subjected to two-way Permutational Multivariate Analysis of Variance (PERMANOVA; Anderson *et al.*, 2008b) to determine whether that variable differed among Year (five levels; 2013/14, 2014/15, 2015/16; 2016/17 and 2017/18) and Month (12 levels; *i.e.* each month of the year), both of which were considered fixed. Note that as the *M. dalli* breeding season finishes in March (Broadley *et al.*, 2017; Crisp *et al.*, 2018b), each Year in the current study comprised the month from April of one calendar year to March in the following year. Prior to running PERMANOVA, the extent of the linear relationship between the $\log_e$ transformed mean and standard deviation for each of the various sets of replicate samples for each variable was examined. This approach was used to determine whether the data for each variable required transformation to meet the test assumption of homogenous dispersions among *a priori* groups and, if so, then to identify the appropriate transformation required (Clarke and Warwick, 2001). This analysis determined that none of the variables required transformation.

In this, and all other tests, the null hypothesis of no significant difference among *a priori* groups was rejected if the test statistic (P) was < 0.05. The percentage contribution made by the mean square for each main effect and interaction term to the total mean squares was calculated to provide an estimate of the relative importance of each term in the model. When a significant difference was detected, in any PERMANOVA test, a pairwise PERMANOVA test, together with a plot of the means and associated 95% confidence limits, was used to identify the pairwise combination of *a priori* groups responsible for that difference. Note that the main focus of these and other PERMANOVA tests was to determine whether there were inter-annual differences, but also investigated the Month main effect and the potentially confounding influence of the Year × Month interaction.

The averaged value for each of water temperature, salinity and dissolved oxygen concentration at the surface and bottom of the water column at each site on each of the weekly sampling occasions were used to make six separate Euclidean distance matrices. These were, in turn, subjected to the same PERMANOVA design used above, only with the additional of a third fixed factor, *i.e.* Region (5 levels; Fig. 3). Visual examination using a Draftsman plot showed that none of these variables required transformation.

The numbers of *M dalli* caught in each sample from nearshore and offshore waters were standardized to a density of prawns 500 m^{-2}, as were those for *P. latisulcatus*. As above, the relationship between the $\log_e$ transformed mean and standard deviation of each species in each water depth was examined to determine whether a transformation was required; this showed that no transformation was necessary. Each of the four data sets was used to construct a Euclidean distance matrix and subjected to three-way PERMANOVA to determine whether the density of either species in either water depth differed significantly among Year (five levels; 2013/14, 2014/15, 2015/16, 2016/17 and 2017/18), Month (six levels; Oct, Nov, Dec, Jan, Feb and Mar) and Subregion (nine levels for the nearshore and eight levels for the offshore, see Fig. 3). All factors were fixed.

One-way Spearman's rank correlation was used to test the hypothesis that the average densities (500 m^{-2}) of *M. dalli* among corresponding sites in the nearshore and offshore waters, averaged over all years, were positively correlated ($p < 0.05$). The same test was also conducted using the average density of *P. latisulcatus*. Note data from the Upper Canning Estuary regions were excluded from this test, as only the nearshore waters were sampled in this region.

Length frequency distributions and egg production estimation

The size structure of the *M. dalli* population during the breeding season (October to March) was examined by constructing carapace length (CL) distributions (1 mm size classes) for the hand trawl nets in the nearshore waters and otter trawl nets in the offshore for each of the five years separately.

Fecundity was estimated for each gravid female *M. dalli* using the methodology developed by Crisp *et al.* (2018b). In brief, this involved converting the CL (mm) of each individual to a total wet weight (g) using (1), estimating the gonad weight from the total weight using (2) and then multiplying this by the fecundity per gram of gonad weight from Crisp *et al.* (2018b), *i.e.* 80,000 ± 7,500 (95% confidence limits), n = 35.

(1) total wet weight (y) and CL (x) of females:

$$y = 0.0037x^{2.4445};\ r^2 = 0.97,\ \mathrm{n} = 1{,}366, \text{ and}$$

(2) gonad weight in grams (y) and total wet weight in grams (x):

$$y = 0.0005x^{3.089};\ r^2 = 0.69,\ \mathrm{n} = 125.$$

Using these equations it was possible to estimate the fecundity of maturing females at a given carapace length. The total number of eggs produced by gravid *M. dalli* in each individual sample from nearshore and offshore waters was standardized to calculate egg production 500 m^{-2}. Note that the monthly estimates of egg production assume that all gravid *M. dalli* will spawn before the next new moon (~28 days later). This assumption was made on the basis that *M. dalli* of similar ovarian condition spawned within ~48 h of transfer to an aquaculture facility, without the need for eyestalk ablation (Crisp et al., 2017a). The total egg production estimates were subjected to the same one-way Spearman's rank correlation test as described earlier for the relationship between total numbers of prawns in the nearshore and offshore waters.

Results

Climatic conditions and water physico-chemistry

Two-way PERMANOVA demonstrated that daily rainfall differed significantly among months but not among years (ranging between 1.5 and 2.1 mm day^{-1}; Fig. 5a) and the Year × Month interaction was not significant (Table 1). The greatest rainfall in each year occurred in the months between May and September, *i.e.* the austral winter and autumn, although there were two notable months where heavy summer rainfall occurred, namely February 2017 and January 2018 (Fig 5b). In these two months mean rainfall was ~ 3 mm day^{-1} compared to 0.39 mm day^{-1} in the corresponding months of the other years.

Maximum and minimum air temperature differed significantly with Year and the Year × Month interaction was also significant (Table 1b,c), due to temperatures being lower in 2016/17 than the other years, *i.e.* ~24 °C *vs* ~26 °C and ~12 °C *vs* ~13 °C, respectively ($P < 0.05$, pairwise PERMANOVA tests, Fig. 5c, 5e). At a finer temporal scale, maximum and minimum temperatures in August, September and October were all significantly lower in 2016/17 than in the other years. This equated to an average of 2.5 to 2.9 °C and 2.1 to 3.3 °C cooler in terms of maximum and minimum temperature, respectively in those three winter months (Fig. 5d, f).

Table 1. Mean squares (MS), percentage contribution of mean squares to the total mean squares (%MS) and significance levels (*P*) from two-way PERMANOVA tests to test whether daily (a) rainfall, (b) maximum air temperature and (c) minimum air temperature measured at Perth Airport differed significantly with Year and Month between April 2013 and March 2018. df = degrees of freedom. Significant results are highlighted in bold.

		(a) Rainfall			(b) Max. air temp.			(c) Min. air temp.		
Source	**df**	**MS**	**%MS**	***P***	**MS**	**%MS**	***P***	**MS**	**%MS**	***P***
Year	4	15.95	3.87	0.756	**231.99**	**5.22**	**0.001**	**126.39**	**5.82**	**0.001**
Month	**11**	**335.47**	**81.34**	**0.001**	**4163.50**	**93.73**	**0.001**	**2003.40**	**92.22**	**0.001**
Year × Month	44	29.03	7.04	0.624	**32.95**	**0.74**	**0.001**	**32.00**	**1.47**	**0.001**
Residual	1766	31.96	7.75		13.43	0.30		10.66		

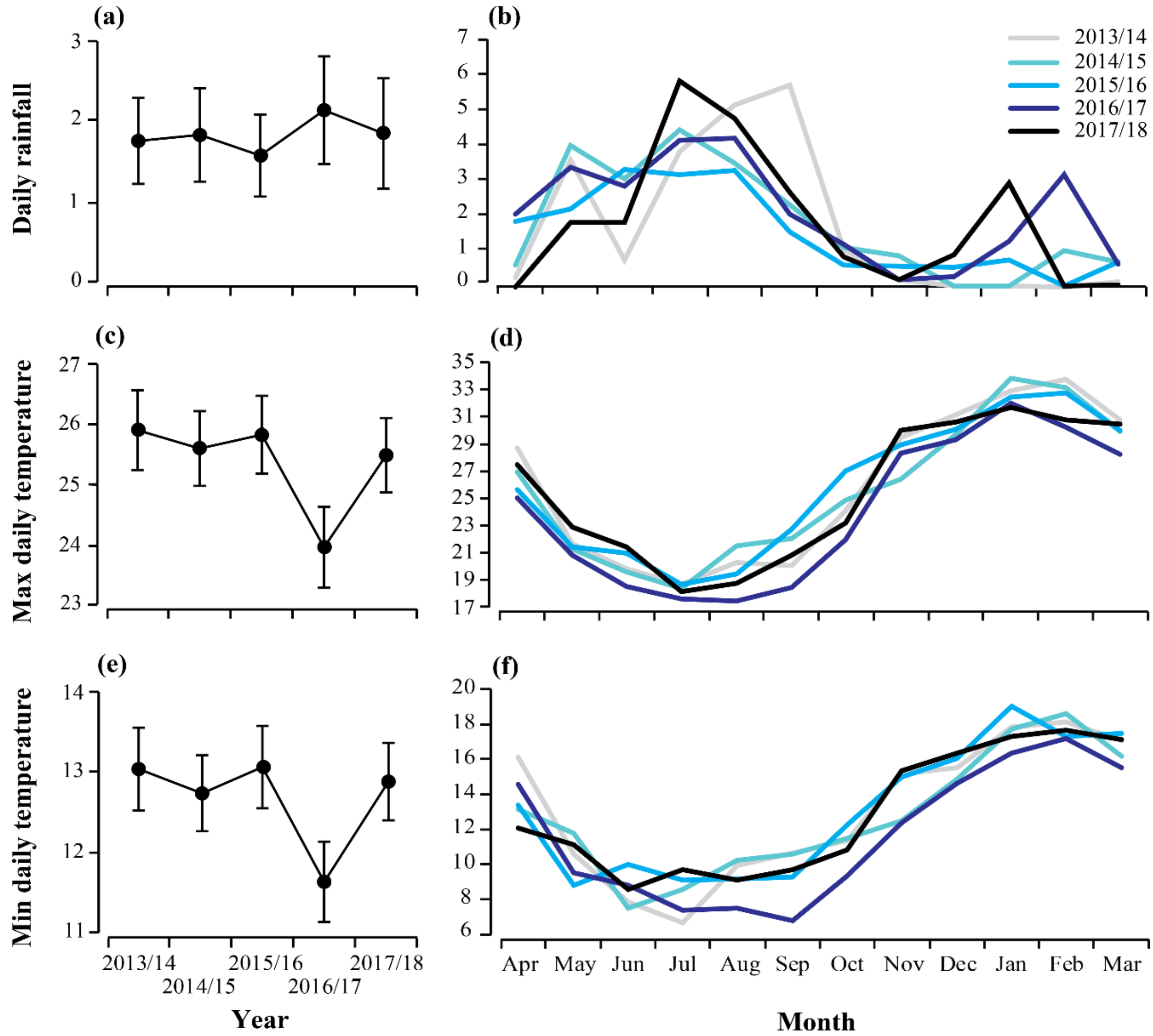

Fig. 5. Mean daily rainfall (mm), maximum and minimum air temperatures (°C) at Perth Airport among (a, c, e) years and (b, d, f) month and year combinations between April 2013 and March 2018. Error bars represent ± 95% confidence limits. Note that, for clarity, error bars are only provided on a, c, and e. Data obtained from the Bureau of Meteorology (http://www.bom.gov.au/climate/data/).

Within the Swan-Canning Estuary, surface and bottom water temperatures differed significantly among years, months, regions and the Year × Month and Month × Region interactions were also significant (Table 2a,b). Among years, temperatures in both water depths were > 20 °C (and usally ~ 20.5 °C) in each year except 2016/17, when they were significantly lower at ~ 19 °C (Fig 6a, b). The Year × Month interaction was caused by surface temperatures in July, August and September of 2016/17 (*i.e.* 13.2, 14.0 and 15.3, respectively) being lower than those of the other years (average = 14.7, 15.8 and 17.3, respectively; Fig. 7a) but not in other months. A trend that also occurred in the bottom waters with values of 15.1, 15.1 and 15.6 recorded in 2016/17 *vs* an average of 16.0, 16.4 and 17.5 in the other years (Fig. 7b).

Table 2: Mean squares (MS), percentage contribution of mean squares to the total mean squares (%MS) and significance levels (*P*) from three-way PERMANOVA to test whether (a) surface and (b) bottom water temperature, (c) surface and (d) bottom salinity and (e) surface and (f) bottom dissolved oxygen concentration differed significantly among years, months and regions of the Swan-Canning Estuary between April 2013 and March 2018. df = degrees of freedom. Significant results are highlighted in bold.

	(a) Surface water temp.				**(b) Bottom water temp.**			
Source	**df**	**MS**	**%MS**	***P***	**df**	**MS**	**%MS**	***P***
Year	**4**	**69.61**	**2.64**	**0.001**	**4**	**38.49**	**2.44**	**0.001**
Month	**11**	**2457.00**	**93.21**	**0.001**	**11**	**1405.70**	**89.06**	**0.001**
Region	**4**	**81.74**	**3.10**	**0.001**	**4**	**102.83**	**6.51**	**0.001**
Year × Month	**44**	**13.72**	**0.52**	**0.001**	**44**	**10.88**	**0.69**	**0.001**
Year × Region	16	0.98	0.04	0.963	16	2.16	0.14	0.083
Month × Region	**44**	**10.42**	**0.40**	**0.001**	**44**	**15.75**	**1.00**	**0.001**
Year× Month × Region	176	0.68	0.03	1.000	176	1.20	0.08	0.912
Residual	2281	1.90	0.07		2046	1.42	0.09	

	(c) Surface salinity				**(d) Bottom salinity**			
Source	**df**	**MS**	**%MS**	***P***	**df**	**MS**	**%MS**	**P**
Year	**4**	**3691.00**	**16.16**	**0.001**	**4**	**691.28**	**5.34**	**0.001**
Month	**11**	**8137.00**	**35.62**	**0.001**	**11**	**1777.90**	**13.73**	**0.001**
Region	**4**	**10237.00**	**44.82**	**0.001**	**4**	**9857.40**	**76.13**	**0.001**
Year × Month	**44**	**575.27**	**2.52**	**0.001**	**44**	**93.05**	**0.72**	**0.001**
Year × Region	**16**	**64.22**	**0.28**	**0.001**	**16**	**190.49**	**1.47**	**0.001**
Month × Region	**44**	**99.85**	**0.44**	**0.001**	**44**	**291.38**	**2.25**	**0.001**
Year × Month × Region	176	17.94	0.08	0.702	176	25.16	0.19	0.085
Residual	2281	19.07	0.08		2046	21.66	0.17	

	(e) Surface diss. oxygen conc.				**(f) Bottom diss. oxygen conc.**			
Source	**df**	**MS**	**%MS**	***P***	**df**	**MS**	**%MS**	***P***
Year	**4**	**19.73**	**6.28**	**0.001**	**4**	**48.70**	**15.55**	**0.001**
Month	**11**	**124.66**	**39.68**	**0.001**	**11**	**14.41**	**4.60**	**0.001**
Region	**4**	**158.26**	**50.37**	**0.001**	**4**	**207.77**	**66.34**	**0.001**
Year × Month	**44**	**2.94**	**0.94**	**0.001**	**44**	**12.64**	**4.04**	**0.001**
Year × Region	**16**	**3.18**	**1.01**	**0.001**	**16**	**10.74**	**3.43**	**0.001**
Month × Region	**44**	**3.75**	**1.19**	**0.001**	**44**	**12.45**	**3.97**	**0.001**
Year × Month × Region	176	0.87	0.28	0.141	**176**	**4.33**	**1.38**	**0.001**
Residual	2281	0.78	0.25		2046	2.14	0.68	

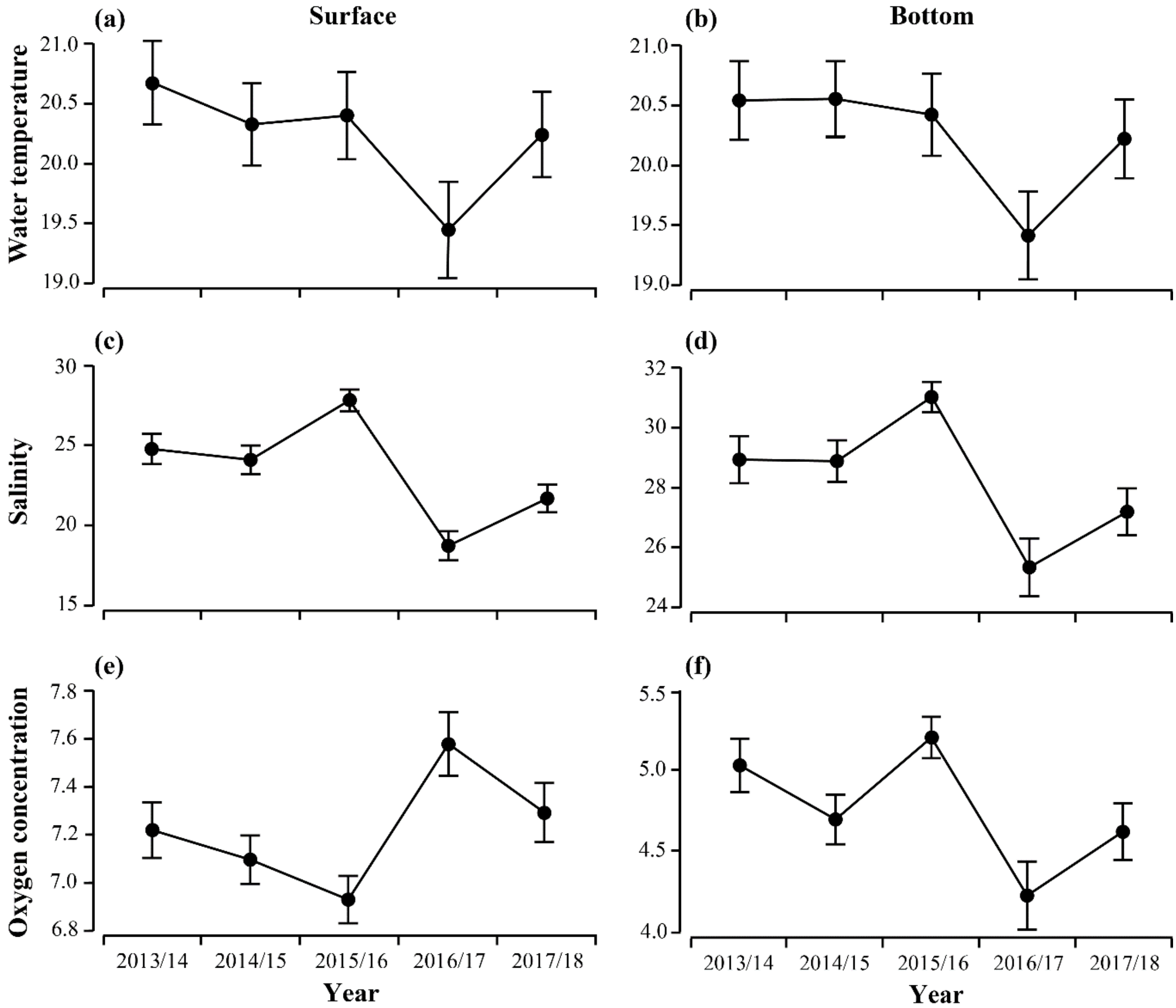

Fig. 6. Mean (± 95% confidence limit) values for (a) surface and (b) bottom water temperature, (c) surface and (d) bottom salinity and (e) surface and (f) bottom dissolved oxygen concentration recorded in the Swan-Canning Estuary in each breeding season between 2013/14 and 2017/18.

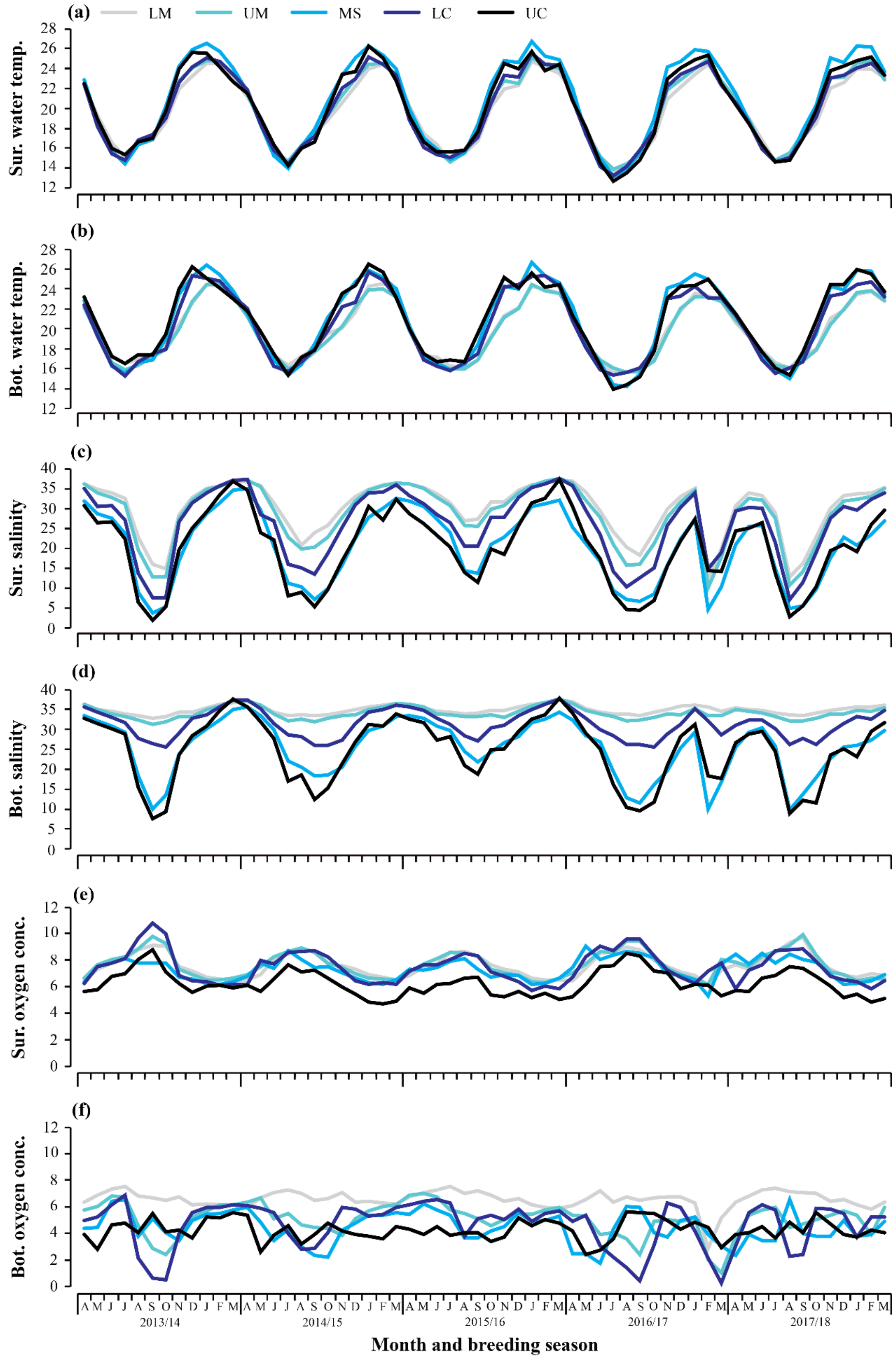

Fig. 7. Mean values for (a) surface and (b) bottom water temperature, (c) surface and (d) bottom salinity and (e) surface and (f) bottom dissolved oxygen concentration recorded in each of the five regions of the Swan-Canning Estuary in month between April 2013 and March 2018. LM, Lower Melville Water; UM, Upper Melville Water; MS, Middle Swan Estuary; LC, Lower Canning Estuary; UC, Upper Canning Estuary.

Water temperature underwent a pronounced seasonal pattern in each region, typically ranging from ~14 °C in June/July to ~26 °C in Janurary/February (Fig. 7b). Seasonal differences were greatest in the Midde Swan Estuary and Upper Canning Estuary and lowest in the Upper and Lower Melville Water and the Lower Canning Estuary. Temperatures in surface waters were almost always > 20 °C between October and April and < 20 °C during May-September (Fig. 7b). Temporal patterns in bottom water temperature mirrored those in the surface waters, but showed less variation, particularly in both Melville Water regions *i.e.* temperatures were typically greater in the bottom than surface waters in the colder months between May and September, and the converse applied in the warmer months between October and March (*cf.* Fig. 7b,d).

Salinities in both the surface and bottom waters were shown by PERMANOVA to differ significantly among years, months, regions and all interactions except the Year × Month × Region interaction were also significant (Table 2c,d). Mean surface salinities were significantly lower in 2016/17 (20.6) and 2017/18 (23.6) than in the three preceeding years (25.6 to 29.0; Fig. 6c); with a similar, albeit less pronounced decline also occuring in the bottom waters (*i.e.* 28.1 and 29.2 in 2016/17 and 2017/18, respectively and 30.6 to 32.2 in the remaining years; Fig. 6d). Surface salinities were markedly lower in February (11.1) and March (16.1) of 2016/17 declining from 31.7 in January of that year; making salinies in those two months 22 and 19 lower than the average of the other years, which contributes the significant Month × Year interaction (Fig. 7c). A second aseasonal decline in surface salinities occurred in January 2017/18, where mean salinitiy was 27.1, compard to 32.5 in other years, which also contributes to the interaction. Declines in salinity were also recorded in the bottom waters in February and March 2016/17 and January 2017/18, although the magnititude of the reduction was far less pronounced (*cf.* Fig. 7c,d).

On average, salinities were greatest in Lower and Upper Melville Water (29.8 and 28.5, respectively), followed by the Lower Canning Estuary (25.9) and least in the Middle Swan Estuary and Upper Canning Estuary (20.2 and 20.1, respectively; Fig. 6c). Among regions and months, surface salinity ranged from 2 in the Upper Canning Estuary during October 2014 to 37.6 in Upper Melville Water and the Lower Canning Estuary in March 2016 (Fig. 6c). Within a lunar month, salinities were most similar across regions during summer/early autumn (December - April), typically differing by < 8, but could be as different as ≥ 15 in September and/or October. The lowest bottom salinity was 7.6 in the Lower Canning Estuary in September 2013, while the highest was 37.8 in that same region during March 2016 (Fig. 7d). Salinities in the bottom waters varied far less than the corresponding surface waters as they were always greater and did not decline as precipitously following rainfall. For example, bottom salinities in Lower Melville Water differed by only 4.6 over the five years, compared to 25.3 in the surface waters of this region and this difference was as high was 35.4 in the Upper Canning Estuary.

PERMANOVA demonstrated that dissolved oxygen concentrations differed significantly among years, months and regions and that all interactions except the Year × Month × Region interaction were significant (Table 2e,f). In the surface waters, mean annual values exceeded 7 mg L^{-1}, but were significantly greater in 2016/17 and 2017/18 than in the previous years (Fig. 6e). Values were lower at the bottom of the water column ranging from 4.3 mg L^{-1} in 2016/17 to 5.5 mg L^{-1} in 2015/16 (Fig. 7e). Concentrations in the surface waters were generally always lower in the Upper Canning Estuary than the other regions, which are all fairly similar, with the highest values in the bottom waters occuring in Lower Melville Water (average = 6.6 mg L^{-1}), compared to values of ~4 mg L^{-1} in the Lower and Upper Canning Estuary and Middle Swan Estuary. The significant Year × Month interation in the bottom waters was due to the occurrence of hypoxic conditions (*i.e.* < 2 mg/L^{-1}; Tweedley *et al.*, 2016a) in the Lower Canning Estuary in September/October 2013 and August/September 2016, in the Middle Swan Estuary between April and June 2016, and the Lower Canning Estuary and Upper Melville Water in February and March 2017 (Fig. 7f).

Overall distribution of **Metapenaeus dalli** *and* **Penaeus latisulcatus**

The mean density of *M. dalli* (500 m^{-2}) in the nearshore waters of the Swan-Canning Estuary over all years ranged from 0.05 to 4.97 (Fig. 8a). Catches were greatest in the Middle Swan and Lower Canning regions and the North Melville Water subregion, with comparatively low and very low densities recorded in the Upper Canning region and Entrance Channel subregion, respectively. At all sites, densities of *M. dalli* were greater in the offshore than the nearshore waters, ranging from 1.68 to 23.57 individuals 500 m^{-2}; Fig 8b). As in the nearshore waters, the Middle Swan and Lower Canning regions yielded the largest catches and, while comparatively few *M. dalli* were obtained from the Entrance Channel, the low densities also extended throughout the deeper parts of Melville Water. There was a strong positive correlation between the average density of *M. dalli* among corresponding sites in nearshore and offshore waters (r = 0.774; p = < 0.001; n = 16).

The pattern of distribution of mean densities of *P. latisculatus* was similar in the nearshore and offshore waters with approximately parallel abundances (Fig. 9), but differed markedly from the patterns for *M. dalli*. Densities were greatest in the Lower Melville Water region and declined progressively in an upstream direction. Individuals of *P. latisulcatus* extended in to the nearshore waters of the Perth Water subregion, but were not recorded in the corresponding deeper, offshore waters and none were caught in the Middle Swan River subregion. Likewise, few individuals penetrated into the nearshore waters of the Upper Canning region and none reached the most upstream site (Fig. 9b). As with *M. dalli*, there was a strong positive correlation between *P. latisulcatus* densities in nearshore and offshore waters (r = 0.773; p = < 0.001; n = 16).

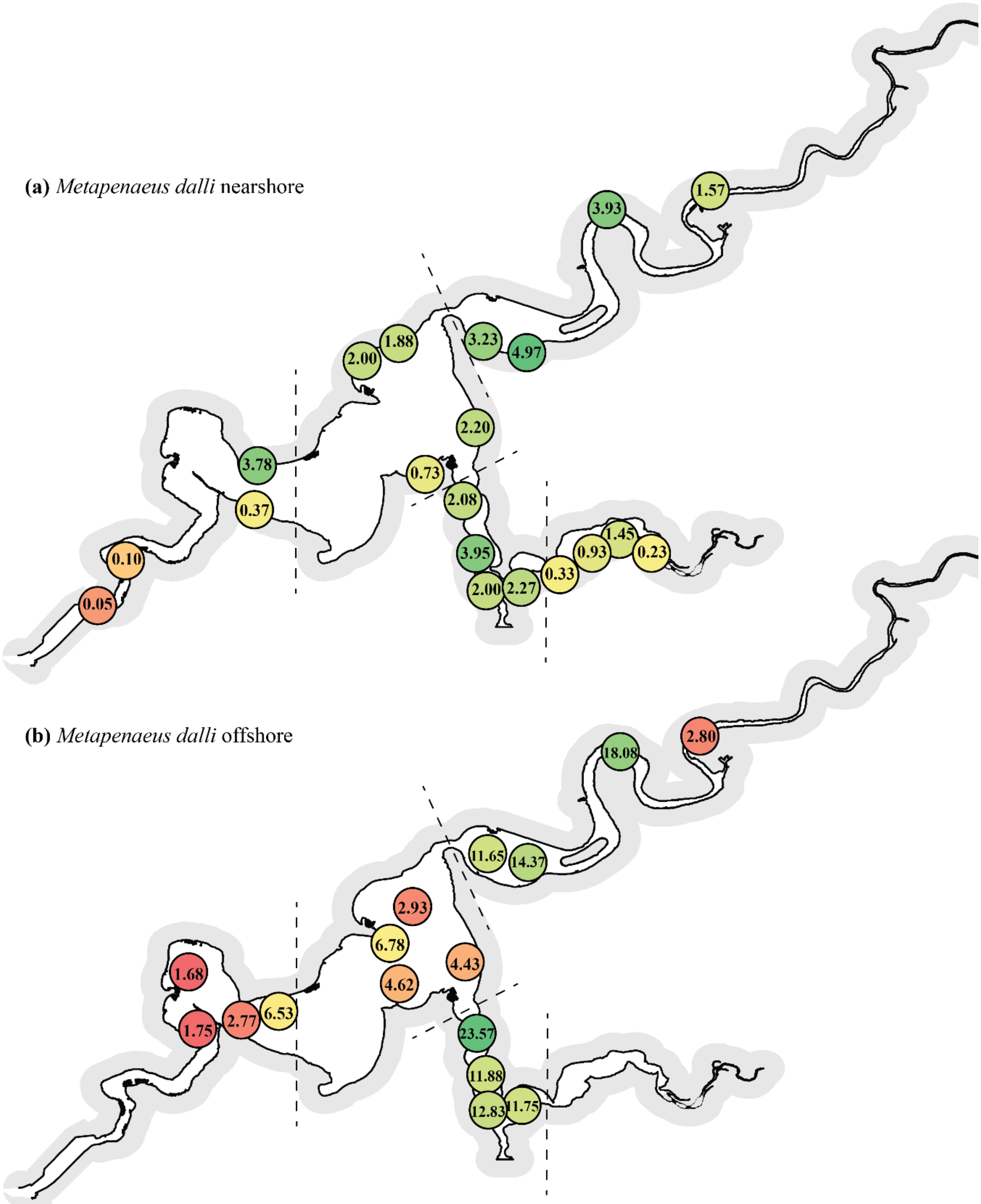

Fig. 8. Heat map showing the mean density (500 m^{-2}) of *Metapenaeus dalli* in each (a) nearshore and (b) offshore site between October and March averaged over the five breeding seasons between 2013/14 and 2017/18. Colour scale is standardized independently for each subfigure, ranging from red for the lowest density to green for the greatest density.

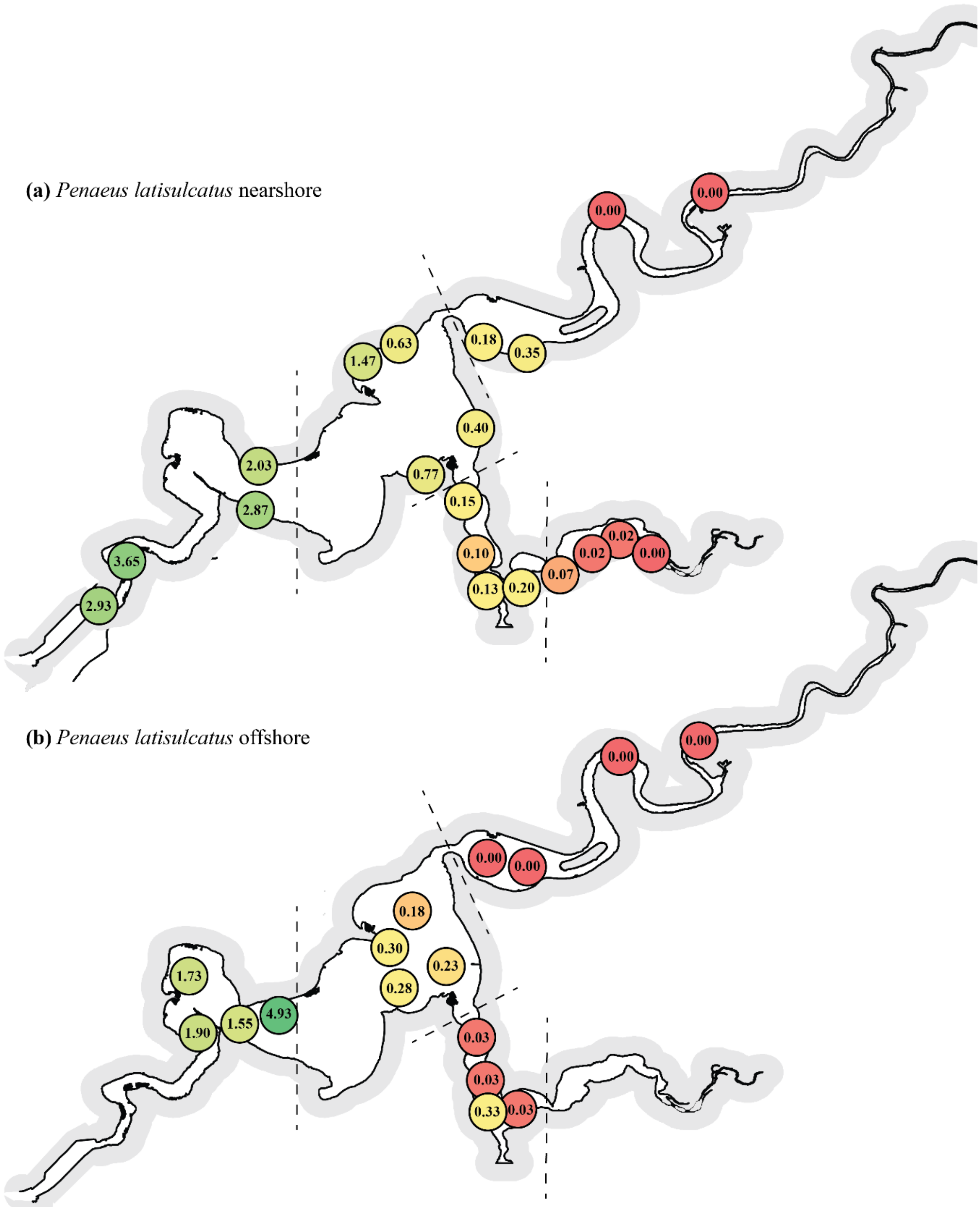

Fig. 9. Heat map showing the mean density (500 m^{-2}) of *Penaeus latisulcatus* in each (a) nearshore and (b) offshore site between October and March averaged over the five breeding seasons between 2013/14 and 2017/18. Colour scale is standardized independently for each subfigure, ranging from red for the lowest density to green for the greatest density.

Density of Metapenaeus dalli *among years, month and subregions*

The density of *M. dalli* in the nearshore waters of the Swan-Canning Estuary differed significantly among all main effects and all interaction terms were also significant (Table 3a). On the basis of the percentage mean squares the largest proportions of the variance were explained by Year (46%), Month (20%) and Subregion (15%), with each of the interactions contributing < ~6% to the total variation. Pairwise PERMANOVA showed that the density of *M. dalli* differed in each year comparison except the first two, *i.e.* 2013/14 and 2014/15 (2.5 and 2.7 *M. dalli* 500 m^{-2}, respectively; Table 4a). Densities increased significantly to 3.9 in 2015/16 before decreasing markedly to only 0.3 in 2016/17 and even more so to 0.1 *M. dalli* 500 m^{-2} in 2017/18 (Fig. 10a). The density of *M. dalli* varied significantly over the breeding season (Table 4b) with, on average, 1.6 individuals 500 m^{-2} in October, increasing to a peak in November of 3.9 before declining in a sequential manner to a minimum of 0.4 individuals 500 m^{-2} in March (Fig. 10b). Subregions in the middle of the Swan-Canning Estuary had the highest mean densities, namely Perth Water, Middle Swan Estuary and the Lower and Middle Canning Estuary, *i.e.* 2.1 to 4.1 *M. dalli* 500 m^{-2}, with very low densities at the most downstream (Entrance Channel, 0.07 *M. dalli* 500 m^{-2}) and upstream sites (Canning Apex 0.8 *M. dalli* 500 m^{-2}; Fig. 10c).

Table 3: Mean squares (MS), percentage contribution of mean squares to the total mean squares (%MS) and significance levels (*P*) from three-way PERMANOVA tests on the density of *Metapenaeus dalli* 500 m^{-2}, caught in (a) nearshore and (b) offshore waters of the Swan-Canning Estuary, over the breeding periods of October to March in 2013/14 to 2017/18. df = degrees of freedom. Significant results are highlighted in bold and those with a %MS ≥ 10 shaded in grey.

	(a) Nearshore				(b) Offshore			
Source	**df**	**MS**	**%MS**	***P***	**df**	**MS**	**%MS**	***P***
Year	**4**	**682**	**45.53**	**0.001**	**4**	**11,763**	**56.60**	**0.001**
Month	**5**	**298**	**19.88**	**0.001**	**5**	**915**	**4.40**	**0.002**
Subregion	**8**	**218**	**14.55**	**0.001**	**7**	**3,656**	**17.60**	**0.001**
Year × Month	**20**	**73**	**4.88**	**0.001**	**20**	**1,467**	**7.06**	**0.001**
Year × Subregion	**32**	**91**	**6.05**	**0.001**	**28**	**1,876**	**9.03**	**0.001**
Month × Subregion	**40**	**62**	**4.16**	**0.001**	**35**	**534**	**2.57**	**0.001**
Year × Month × Subregion	**160**	**49**	**3.26**	**0.002**	**140**	**398**	**1.92**	**0.001**
Residual	930	25	1.70		720	173	0.83	

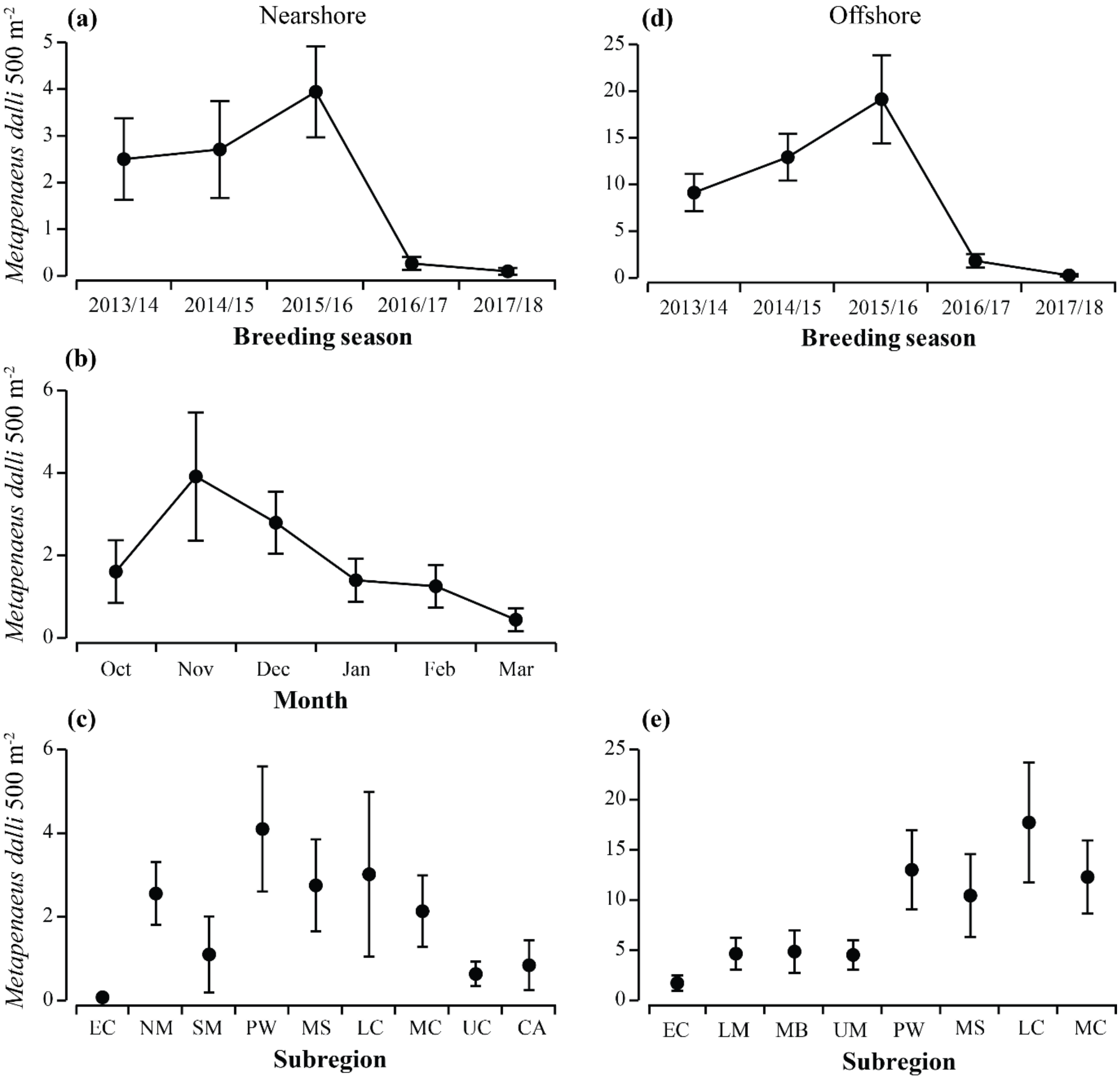

Fig. 10. Mean density (500 m^{-2}) of *Metapenaeus dalli* in (a) years, (b) months and (c) subregions in nearshore waters and (d) years and (e) subregions in the offshore waters of the Swan-Canning Estuary. Data based on monthly sampling between October and March in each of five years between 2013/14 and 2017/18. Error bars represent ± 95% confidence limits. EC = Entrance Channel; NM = North Melville Water; SM = South Melville Water; MS, Middle Swan Estuary; LC, Lower Canning Estuary; UC, Upper Canning Estuary; CA = Canning Apex; LM, Lower Melville Water; MB, Matilda Bay; UM, Upper Melville Water; MC = Middle Canning Estuary.

Table 4: *t* values and significance levels (*P*) from pairwise PERMANOVA tests on the density of *Metapenaeus dalli* 500 m^{-2} in nearshore waters of the Swan-Canning Estuary, over the breeding periods of October to March in 2013/14 to 2017/18, among (a) years, (b) months and (c) subregions and in offshore waters of the same estuary among (d) years and (e) subregions. Non-significant results shaded in grey and the extent of significant difference denoted in superscript, $^{3} = P < 0.05$, $^{2} = P < 0.01$ and $^{1} = P < 0.001$. EC = Entrance Channel; NM = North Melville Water; SM = South Melville Water; MS, Middle Swan Estuary; LC, Lower Canning Estuary; UC, Upper Canning Estuary; CA = Canning Apex; LM, Lower Melville Water; MB, Matilda Bay; UM, Upper Melville Water; MC = Middle Canning Estuary.

Nearshore waters

(a) Year	13/14	14/15	15/16	16/17
14/15	0.50			
15/16	3.19^{2}	2.37^{1}		
16/17	4.99^{3}	4.94^{3}	10.63^{3}	
17/18	5.41^{3}	5.30^{3}	11.16^{3}	2.61^{2}

(b) Month	Oct	Nov	Dec	Jan	Feb
Nov	2.91^{2}				
Dec	2.89^{2}	1.30			
Jan	0.57	3.33^{1}	3.99^{1}		
Feb	0.87	3.51^{1}	4.52^{1}	0.34	
Mar	3.52^{1}	4.76^{1}	7.54^{1}	3.92^{1}	4.16^{1}

(c) Subregion	EC	NM	SM	PW	MS	LC	MC	UC
NM	6.20^{1}							
SM	1.81^{3}	2.63^{2}						
PW	7.45^{1}	2.64^{2}	4.23^{1}					
MS	7.22^{1}	0.39	2.59^{2}	2.07^{3}				
LC	3.23^{1}	0.56	2.09^{3}	1.02	0.27			
MC	7.17^{1}	0.92	1.70	3.23^{1}	1.32	0.93		
UC	4.07^{2}	4.66^{1}	0.81	6.24^{1}	5.40^{1}	2.59^{1}	4.77^{2}	
CA	3.05^{1}	3.85^{1}	0.43	5.49^{1}	4.29^{1}	2.30^{1}	3.41^{2}	0.74

Offshore waters

(d) Year	13/14	14/15	15/16	16/17
14/15	3.01^{2}			
15/16	5.20^{1}	3.26^{1}		
16/17	7.78^{1}	12.36^{1}	10.13^{1}	
17/18	9.70^{1}	14.54^{1}	11.13^{1}	6.65^{1}

(e) Subregion	EC	LM	MB	UM	PW	MS	LC
LM	3.94^{1}						
MB	3.41^{1}	0.19					
UM	5.08^{1}	0.15	0.34				
PW	8.76^{1}	5.87^{1}	5.35^{1}	6.36^{1}			
MS	4.50^{1}	2.85^{2}	2.65^{3}	3.00^{2}	1.12		
LC	8.63^{1}	6.70^{1}	6.35^{1}	7.00^{1}	2.13^{3}	2.75^{3}	
MC	8.54^{1}	5.54^{1}	5.02^{1}	6.04^{1}	0.41	0.82	2.48^{3}

In offshore waters, the density of *M. dalli* differed among all main effects and the interaction terms were all significant, with Year and Subregion explaining the largest proportions of the variance (*i.e.* 57 and 18%, respectively; Table 3b). The interaction terms each accounted for < ~9% of the total mean squares. Pairwise PERMANOVA demonstrated that the density of *M. dalli* differed in each year, increasing sequentially from 9.1 *M. dalli* 500 m^{-2} in 2013/14 to a peak of 19.1 *M. dalli* 500 m^{-2} in 2015/16, before undergoing a dramatic decline to only 1.8 and 0.3 *M. dalli* 500 m^{-2} in 2016/17 and 2017/18, respectively (Fig. 10d). Densities were lowest and highest in the Entrance Channel and Lower Canning Estuary, respectively (1.7 and 17.7 *M. dalli* 500 m^{-2}), with these subregions being statistically different from all others. The remaining subregions formed one of two groups, the first with low intermediate densities of 4.5 to 4.9 *M. dalli* 500 m^{-2} comprised those located in Melville Water, while the second group of subregions, namely Perth Water, Middle Swan Estuary and Lower Canning Estuary yielded, on average, high intermediate densities (10.4 to 13.0 individuals 500 m^{-2}; Fig. 10e). The monthly pattern in density in the offshore waters followed that in nearshore waters, being greatest in November and lowest in February and March (12.3, 5.8 and 6.3 *M. dalli* 500 m^{-2}, respectively; data not shown) but Month accounted for only ~4% of the total mean squares in the offshore compared with 19.9% in the nearshore.

On the basis of percentage change in catches from 2013/14 (a surrogate for the base level prior to restocking), the density of *M. dalli* in nearshore waters had increased by 58% by 2015/16, before declining massively to 11% of the starting population in 2016/17, which decreased to further to only 4% of the 2013/14 density in 2017/18 (Fig. 11). In offshore waters, mean densities followed a similar pattern of increase followed by precipitous decline: first, a progressive increase to 141 and 209% in 2014/15 and 2015/16, respectively, and then a marked decline in 2016/17 (20% of the 2013/14 level) and 2017/18 (only 3% of that in 2013/14; Fig. 11). A total of 53 and 215 gravid *M. dalli* were collected in nearshore and offshore waters in the 2013/14 breeding season, with these numbers increasing to 213 and 253, respectively in 2015/16; percentage increases of 302 and 18%. However, only 23 and 2 gravid females were caught in nearshore waters in 2016/17 (44 and 4% of the 2013/14 total) and 2017/18, respectively, with 17 and 4 collected in the corresponding offshore waters in those two seasons (8 and 2% of the 2013/14 total).

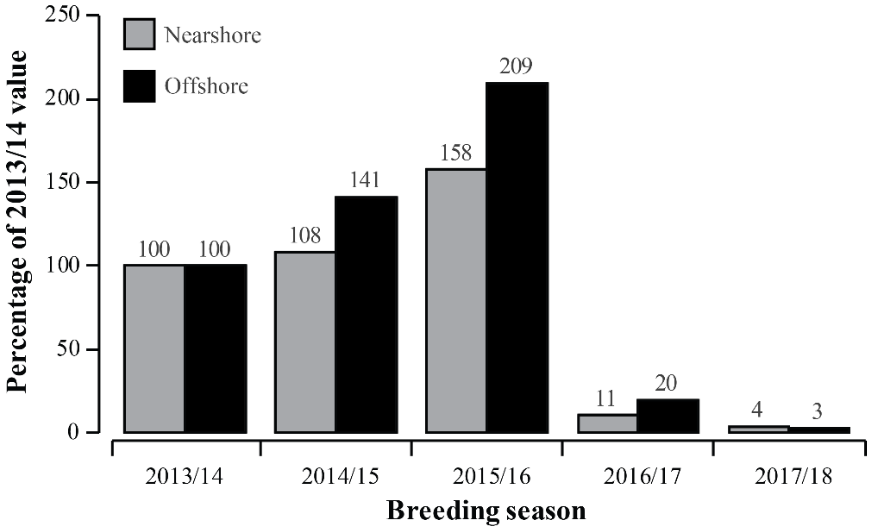

Fig. 11. Percentage change in the density of *Metapenaeus dalli* in nearshore and offshore waters of the Swan-Canning Estuary from the 'base level' in 2013/14.

Carapace length frequency distributions of **Metapenaeus dalli**

The carapace length (CL) frequency of female prawns in the nearshore waters ranged from 2 mm (2014/15 breeding season) to 30 mm (2015/16 breeding season). During the first three years of the study, a good range of carapace lengths were recorded, particularly between 10 and 25 mm CL, while in the last two years, the CL distributions were more disjoint because of small sample sizes, particularly in 2017/18 (Fig. 12). Very few mature female prawns were caught in these last two years (22 females > 20 mm CL in 2016/17 and 3 in 2017/18). The modal size of females in 2015/16 was between 20 and 22 mm CL, larger than in the two previous years (18 to 20 mm and 19 to 20 mm). The modal size of males was smaller than females and showed the same pattern of variation between 2015/16 and the previous two years – modal size in 2015/16 = ~17-18 mm CL compared with 15-16 mm in 2014/15 and 2013/14 (Fig. 12).

Two modes were evident in the carapace length distributions of females prawns caught in otter trawls in the offshore waters in 2013/14 and 2014/15, with the first mode at ~ 10 mm and the second at 19-21 mm CL (Fig. 13). These modes were less evident in the following four years. In contrast to the size distribution in the nearshore waters, in 2015/16 the CL distributions of males and females did not appear to be larger than in the previous two years. Few females larger ≥ 20 mm CL were caught in 2016/17 (~50) and 2017/18 (~16; Fig. 13).

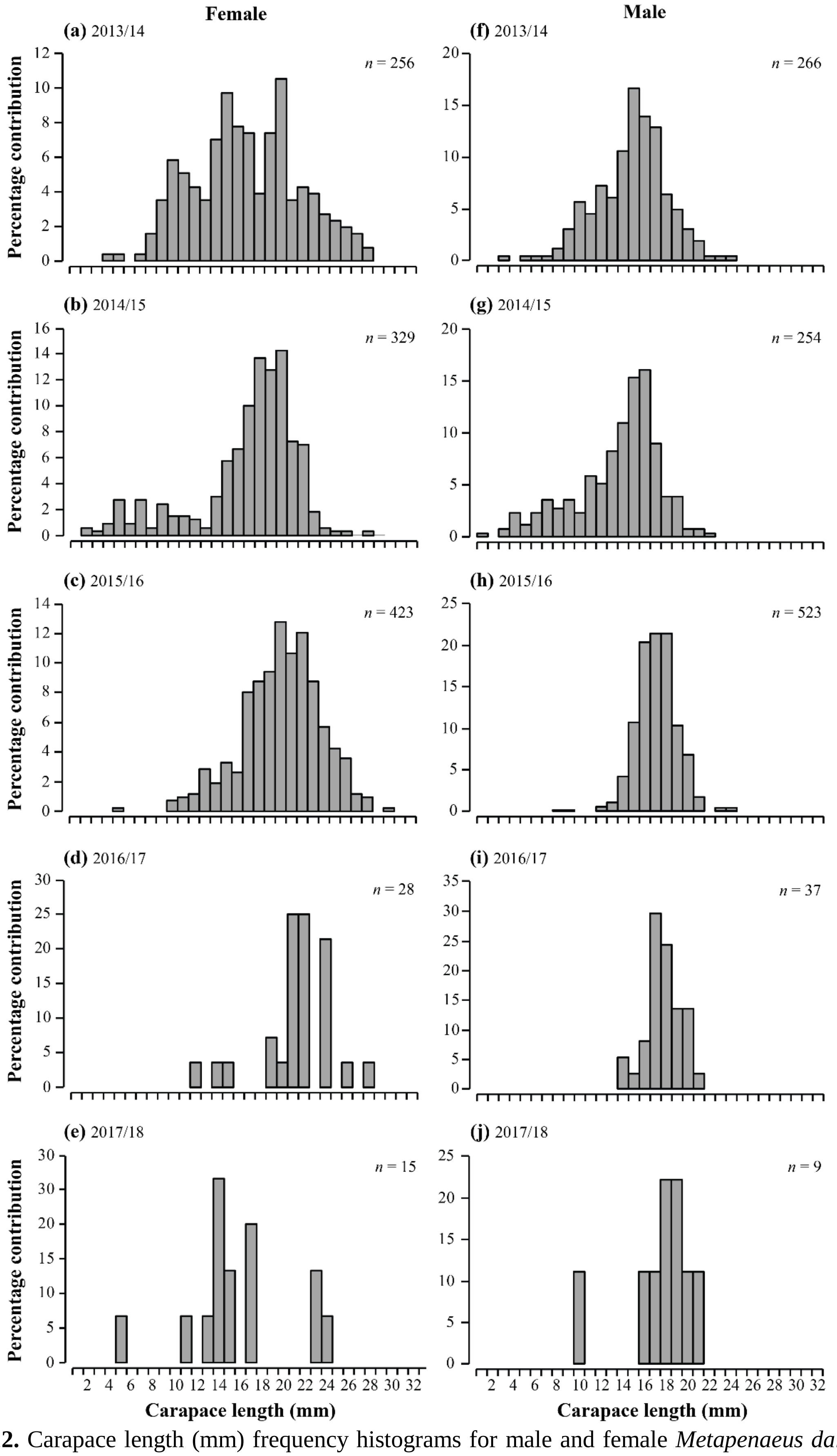

Fig. 12. Carapace length (mm) frequency histograms for male and female *Metapenaeus dalli* in 1 mm length classes from the nearshore waters of the Swan-Canning Estuary between October and March of (a, b) 2013/14, (c, d) 2014/15, (e, f) 2015/16, (g, h) 2016/17 and (i, j) 2017/18.

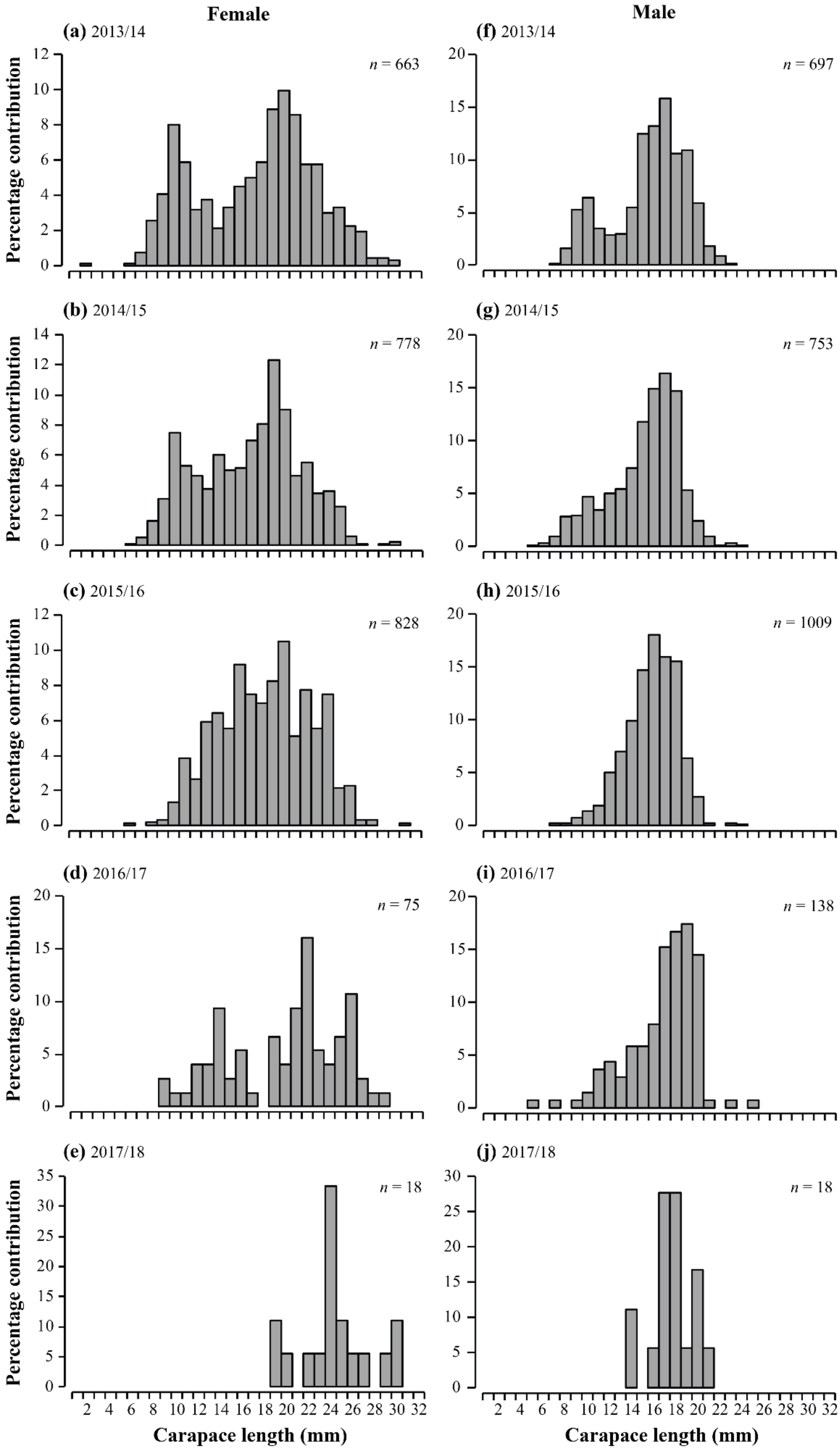

Fig. 13. Carapace length (mm) frequency histograms for male and female *Metapenaeus dalli* in 1 mm length classes from the offshore waters of the Swan-Canning Estuary between October and March of (a, b) 2013/14, (c, d) 2014/15, (e, f) 2015/16, (g, h) 2016/17 and (i, j) 2017/18.

Egg production

The estimated total number of eggs 500 m^{-2} produced by gravid *M. dalli* in nearshore waters over the duration of the study ranged from 0 in sites in the Entrance Channel and the upper most site in the Canning Estuary, to 1,243,508 at Garrett Road Bridge in the Middle Swan Estuary (Fig. 14a). Other sites that yielded relatively large quantities of eggs were Maylands, also in the Middle Swan Estuary, and Canning Bridge and Deep Water Point in the Lower Canning Estuary (all 650,000 – 950,000), followed by Dalkeith (400,000) and sites in Perth Water (234,000 – 350,000). Relatively few eggs were produced at the remaining sites in Melville Water and, in particular, Ardross and Como.

In offshore waters, as in the nearshore, the lowest estimated egg production was in the Entrance Channel (as in the nearshore), but the areas with the largest numbers of eggs in the offshore (*i.e.* > 950,000 eggs) were more spread out into 'local hotspots' than in the nearshore (Fig. 14b). These areas of high egg production included two sites in the Lower Canning and Middle Swan Estuary regions, as well as Dalkeith in Lower Melville Water. Despite the more variable spatial pattern of egg production in the offshore than nearshore waters, there was a significant correlation between total egg production among sites in the two water depths ($r = 0.528$; $p = 0.035$; $n = 16$).

In nearshore waters, typically the monthly egg production 500 m^{-2} peaked twice during most breeding seasons, once in November/December and again in February (Fig. 15a). The timing and magnitude of this production changed markedly among years. Thus, it was greatest in 2015/16, due to peaks in November, December and most notably February and also relatively high in the preceding year due to relatively large numbers of eggs being produced in November (Fig 15a). The cumulative egg production each breeding season increased sequentially from ~5,600 in 2013/14 to 22,600 in 2014/15 through to a peak of 114,000 500 m^{-2} in 2015/16, 20 times larger than in 2013/14 (Fig. 15b). Production then decreased by over 90% to 9,000 in 2016/17 and a further 90% in the following year to only ~ 900, *i.e.* < 1% of the egg production 500 m^{-2} in 2015/16 and < 20% of that in 2013/14.

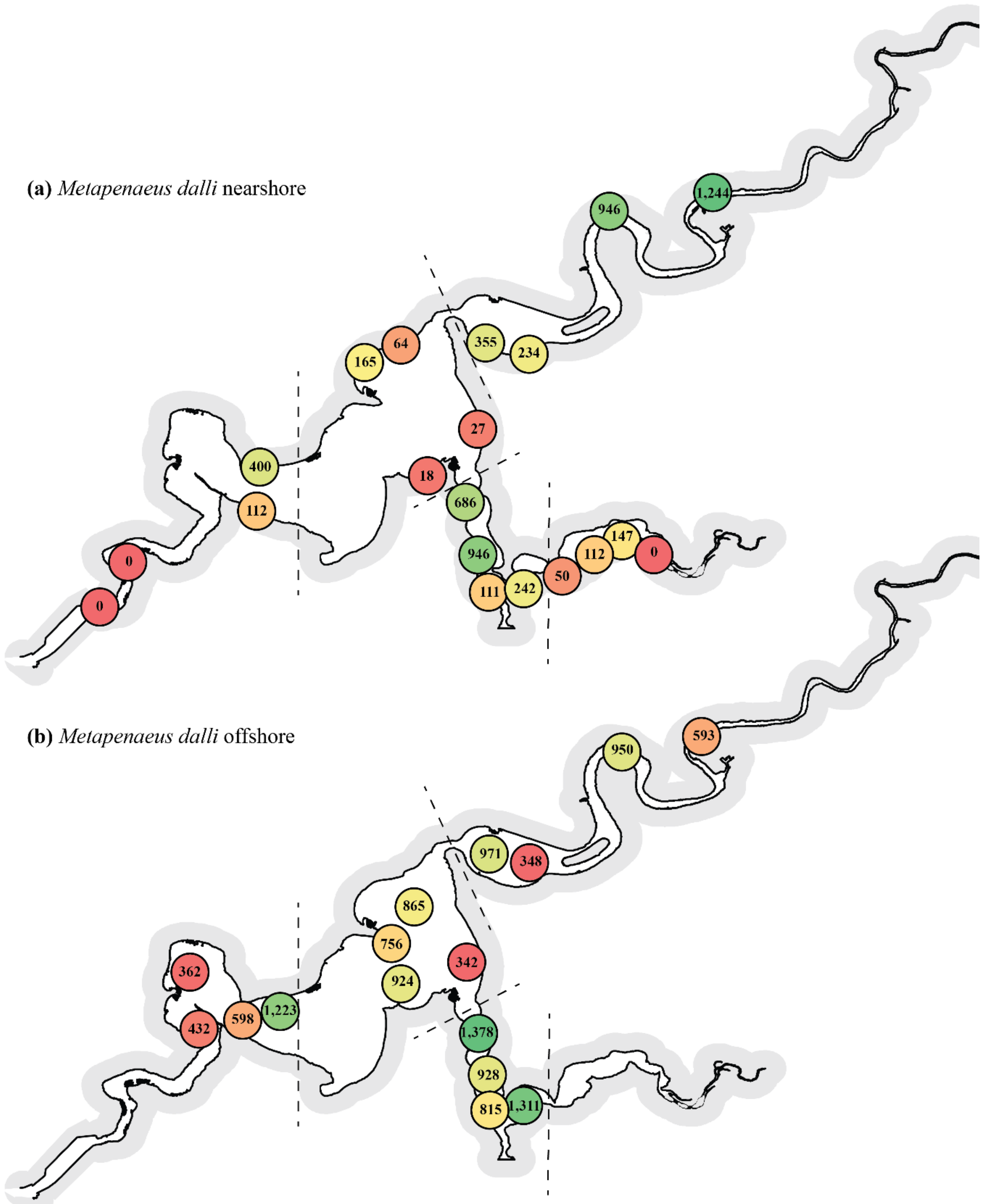

Fig. 14. Heat map showing the total number of eggs produced by gravid *Metapenaeus dalli* (thousand eggs 500 m^{-2}) at each site in the (a) nearshore and (b) offshore waters Swan-Canning Estuary over the five breeding seasons between October and March in each year between 2013/14 and 2017/18.

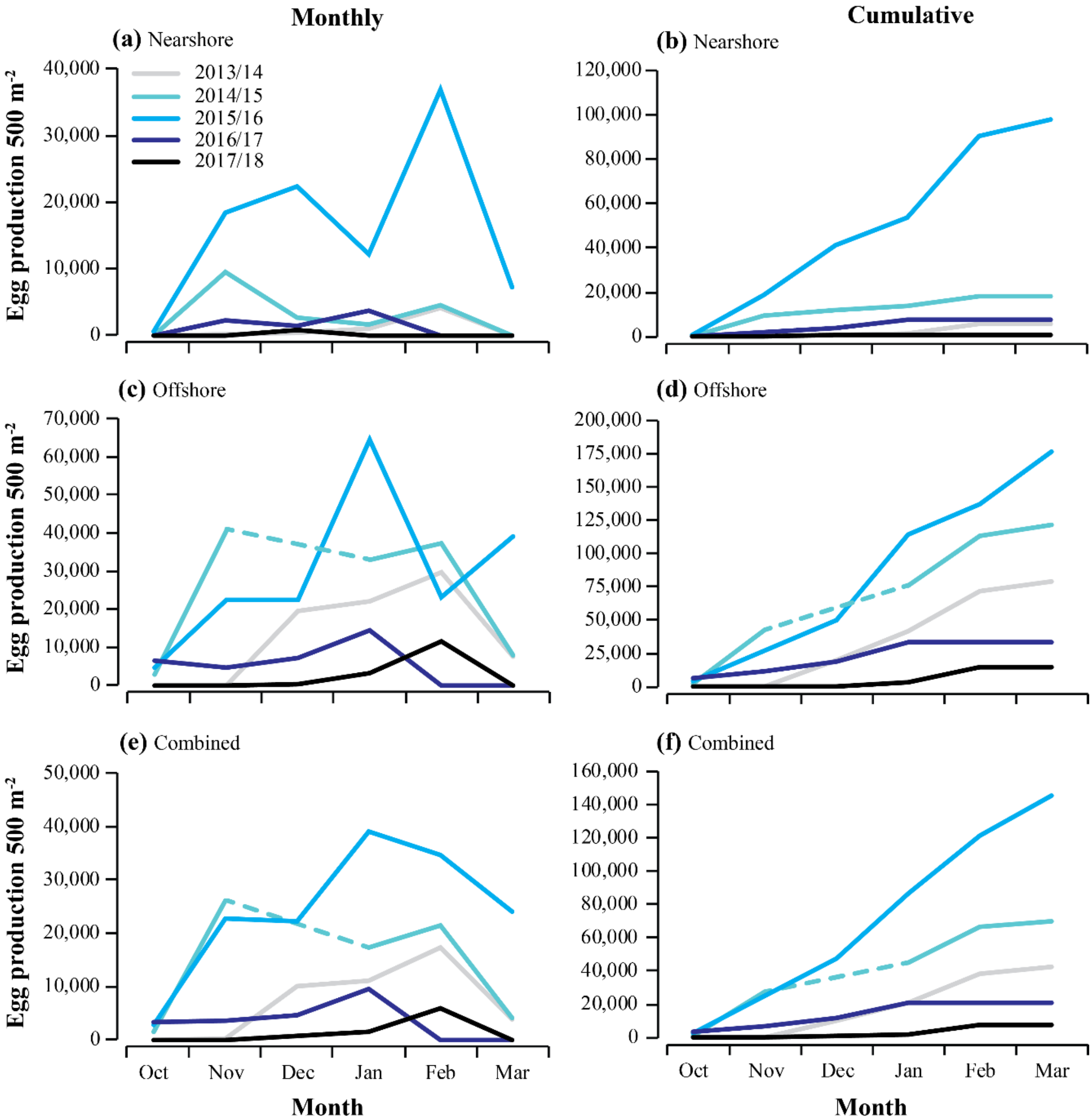

Fig. 15. Average egg production by female *Metapenaeus dalli* 500 m^{-2} per month (a, c, e) and cumulative (b, d, f) in (a, b) nearshore, (c, d), offshore and (e, f) combined (nearshore and offshore) waters of the Swan–Canning Estuary. Dashed line indicates absence of values in offshore waters due to boat breakdown in December 2014.

Production in the offshore waters peaked in different months in the various years, occurring in November and February in 2014/15, in December and February in 2013/14 and then in January in 2015/16 and 2016/17 and in February in 2017/18 (Fig. 15c). As in the nearshore waters, production increased sequentially from 2013/14 to a peak in 2015/16, albeit the production in the latter year was not as disproportionally high (only 2.2 and 1.4 times greater than the preceding two years, respectively). When production was averaged across nearshore and offshore waters, it was greatest in 2015/16, due to a larger numbers of eggs being produced in November and a second peak in January and February (Fig. 15e,f).

Most egg production in the nearshore waters occurred in the Lower Canning or Middle Swan Estuary regions, with notable contributions from Lower Melville Water in 2013/14 and 2017/18 when egg production was only recorded from this region (Fig. 16). The location and timing of production differed among years. In both 2014/15 and 2015/16 production peaked the Lower Canning Estuary in November, with it also continuing in to December of the latter year (Fig. 16c, d). In 2016/17, however, production in this region peaked later in January, with the production in November occurring in the Middle Swan Estuary. Limited production occurred in the Upper Canning until January in 2013/14, when it was also recorded in Lower Melville Water and in the Middle Swan in the following month (Fig. 14a). In 2017/18, egg production was very limited, occurring only in Lower Melville Water and then only in December (Fig. 14i, j).

Regions of high egg production in offshore waters differed across the years, being greatest in the Lower and Upper Melville Water in 2013/14, the Lower Canning Estuary in 2014/15 and 2016/17 and in the Middle Swan Estuary in both 2016/17 and 2017/18 (Fig. 17). With the exception of 2014/15, the timing of egg production in the offshore waters of each region was fairly similar in each year. Thus, occurring in all regions between December and February in 2013/14, in January and March of 2015/16 and January and February of 2016/17 and 2017/18, respectively. In 2014/15, egg production in the Lower Canning Estuary was greatest in November and February compared with January for Upper Melville Water. In the last three years of the study, there was limited egg production in Lower and Upper Melville Water, except for Upper Melville Water in 2017/18 (Fig. 17).

On the basis of percentage change in egg production from 2013/14 (a surrogate for the base level prior to restocking), estimated production in nearshore waters increased by 300% in 2015/16 and 1,912% in 2015/16. Although egg production in 2016/17 was greater than in 2013/14, the magnitude of the increase was less than previous year at 60%. However, production in 2017/18 was only 16% of that in 2013/14. Similar, but less marked trends in egg production were recorded in offshore waters between 2013/14 and 2017/18: it increased by 54% in 2014/15 and 124% in 2015/16, but and was only 42 and 19% of the 2013/14 value in 2016/17 and 2017/18, respectively.

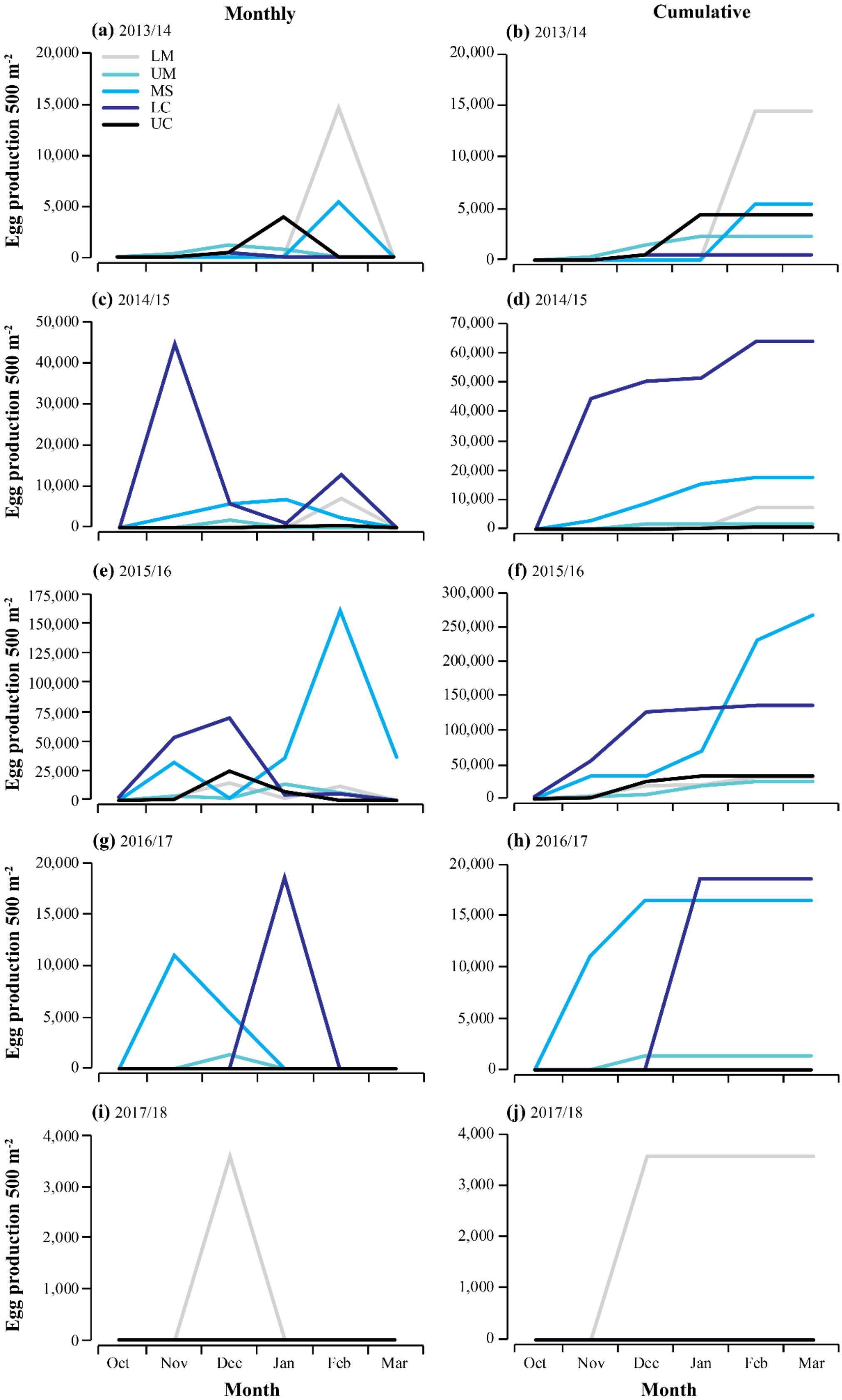

Fig. 16. Average egg production by female *Metapenaeus dalli* 500 m^{-2} per month (a, c, e, g, i) and cumulative (b, d, f, h, j) in the nearshore waters of each of the five regions of the Swan-Canning Estuary in (a, b) 2013/14, (c, d) 2014/15, (e, f) 2015/16, (g, h) 2016/17 and (i, j) 2017/18. LM = Lower Melville Water; UM = Upper Melville Water; MS = Middle Swan; LC = Lower Canning Estuary; UC = Upper Canning Estuary.

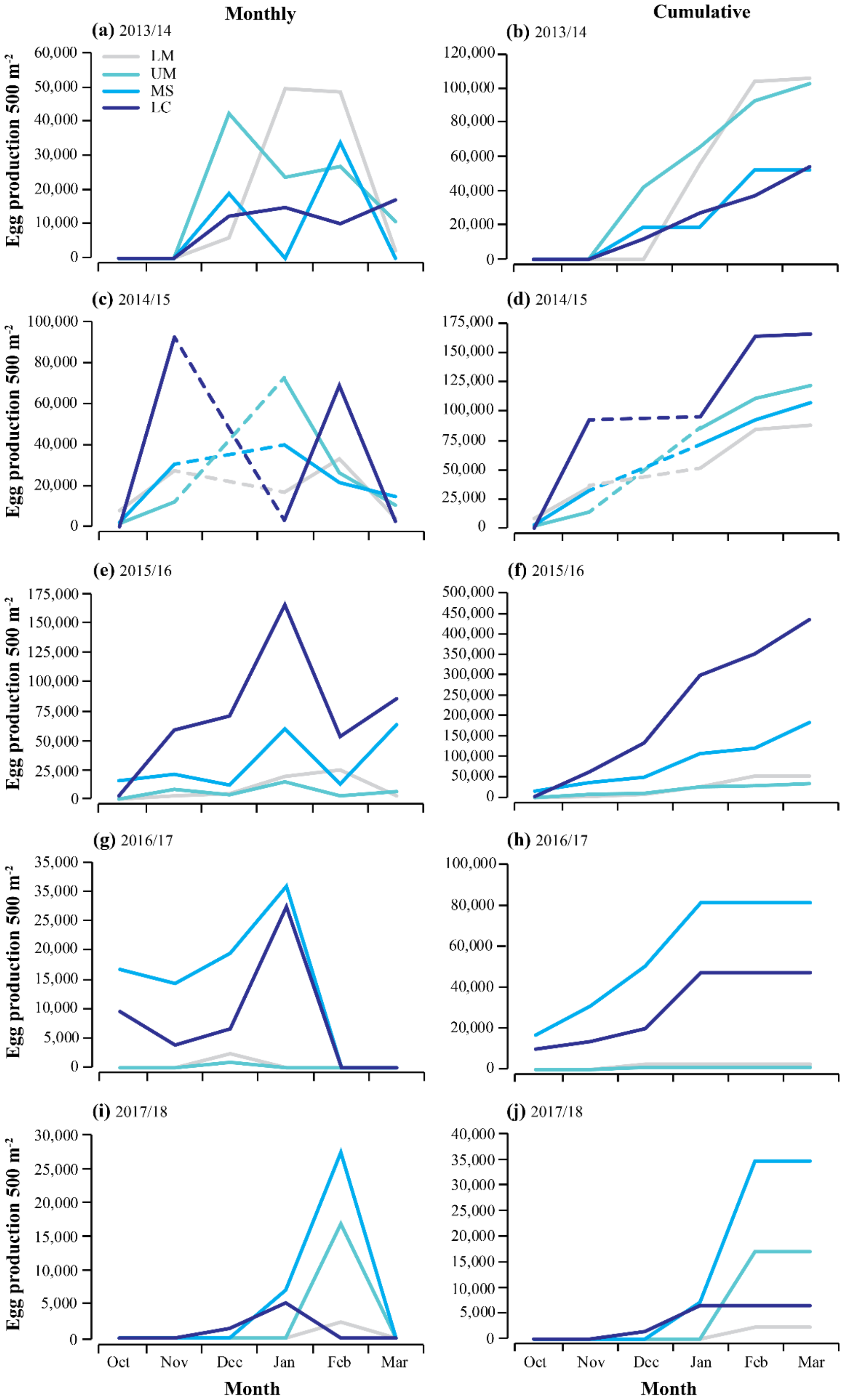

Fig. 17. Average egg production by female *Metapenaeus dalli* 500 m^{-2} per month (a, c, e, g, i) and cumulative (b, d, f, h, j) in the offshore waters of each of the five regions of the Swan-Canning Estuary in (a, b) 2013/14, (c, d) 2014/15, (e, f) 2015/16, (g, h) 2016/17 and (i, j) 2017/18. Dashed line indicates absence of values in offshore waters due to boat breakdown in December 2014. LM = Lower Melville Water; UM = Upper Melville Water; MS = Middle Swan; LC = Lower Canning Estuary.

Density of* Penaeus latisulcatus *among years, month and subregions

The density of *P. latisulcatus* in the nearshore waters differed significantly among all main effects, except Month, and all interaction terms were also significant (Table 5a). The largest proportions of the total mean squares were explained by Subregion (52%) and Year (22%). Among years, densities were greatest in 2017/18 and 2013/14 (1.9 and 0.8 individuals 500 m^{-2}, respectively), with each of these years have significantly greater densities than in the other three years (0.3 to 0.6 individuals 500 m^{-2}, Fig. 18a, Table 6a). The mean density of *P. latisulcatus* was significantly greater in the Entrance Channel (3.3 individuals 500 m^{-2}) than all other regions (< 0.2 to 1.3 to < 0.2 individuals 500 m^{-2}, Fig. 18b, Table 6b). Densities in Northern and Southern Melville Water were also significantly greater than in the other regions (*i.e.* 1.3 *vs* < 0.2 individuals 500 m^{-2}; Fig. 18b). Densities were similar among months, being, on average, 0.8 individuals 500 m^{-2} (data not shown).

In offshore waters, the density of *P. latisulcatus* differed among all main effects and all interaction terms, except Year × Month, were also significant. Each main effect explained ≥ ~10% of the total mean squares (Table 5b). Densities were typically significantly greater in 2013/14 than the other breeding seasons (*i.e.* 1.3 *vs* 0.2 to 0.8 *P. latisulcatus* 500 m^{-2}; Fig 18c; Table 6c). Generally densities in January, February and March were greater than those in November and December (Fig. 18d). Mean density decreased markedly with distance from the mouth of the estuary, with densities in the two most downstream regions (Entrance Channel and Lower Melville Water) not being significantly different from each other (3.2 and 1.8 *P. latisulcatus* 500 m^{-2}), but being significantly greater than all other regions (< 0.3 *P. latisulcatus* 500 m^{-2}; Fig. 18e; Table 6e).

Ratio of Metapenaeus dalli and Penaeus latisulcatus

During the first three breeding seasons (2013/14 to 2015/16), 77% of the penaeids caught in the nearshore waters of the Swan-Canning Estuary were *M. dalli* (Fig 19a). This proportion was typically greater during the first three to four months of these breeding seasons, *i.e.* > 85%, but then declined sequentially reaching a minima in March (ranging from 33% in 2013/14 to 63% in 2015/16).

Table 5: Mean squares (MS), percentage contribution of mean squares to the total mean squares (%MS) and significance levels (*P*) from three-way PERMANOVA tests on the density of *Penaeus latisulcatus* 500 m^{-2}, caught in (a) nearshore and (b) offshore waters of the Swan-Canning Estuary, over the breeding periods of October to March in 2013/14 to 2017/18. df = degrees of freedom. Significant results are highlighted in bold and those with a %MS ≥ 10 shaded in grey.

	Nearshore				Offshore			
Source	**df**	**MS**	**%MS**	***P***	**df**	**MS**	**%MS**	***P***
Year	**4**	**65.2**	**22.44**	**0.001**	**4**	**27.6**	**9.38**	**0.007**
Month	5	11.9	4.09	0.070	**5**	**37.3**	**12.70**	**0.001**
Subregion	**8**	**152.1**	**52.34**	**0.001**	**7**	**163.1**	**55.30**	**0.001**
Year × Month	**20**	**12.4**	**4.25**	**0.006**	20	9.2	3.14	0.548
Year × Subregion	**32**	**26.7**	**9.20**	**0.001**	**28**	**20.3**	**6.88**	**0.001**
Month × Subregion	**40**	**8.7**	**3.00**	**0.033**	**35**	**14.0**	**4.75**	**0.017**
Year × Month × Subregion	**160**	**7.5**	**2.60**	**0.041**	**140**	**13.7**	**4.63**	**0.001**
Residual	930	6.0	2.07		720	9.5	3.23	

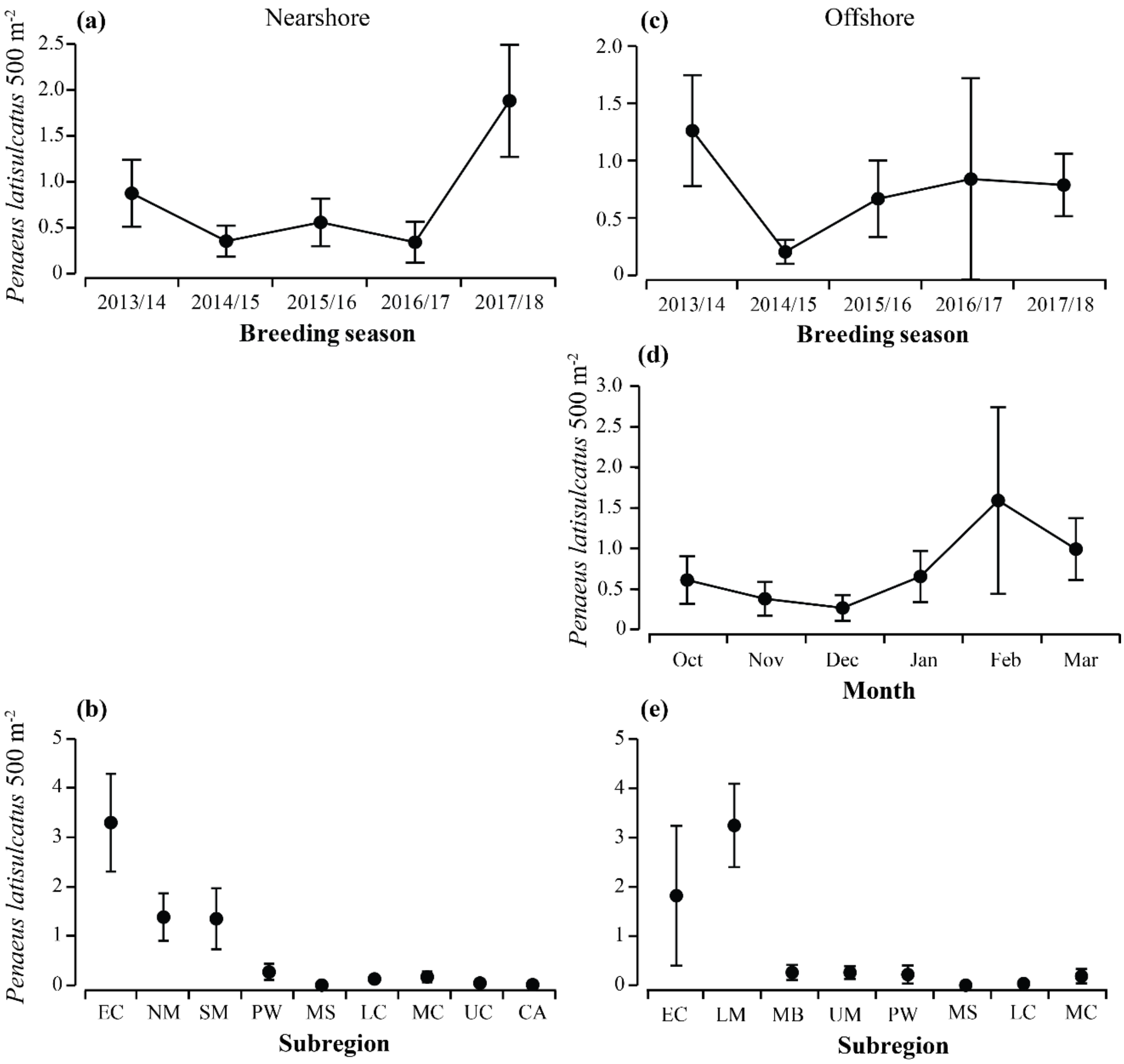

Fig. 18. Mean density (500 m^{-2}) of *Penaeus latisulcatus* in among (a) years and (d) subregions in nearshore waters and (b) years, (c) months and (e) subregions in the offshore waters of the Swan-Canning Estuary. Data based on monthly sampling between October and March in each of five years between 2013/14 and 2017/18. Error bars represent ±95% confidence limits. EC = Entrance Channel; NM = North Melville Water; SM = South Melville Water; MS, Middle Swan Estuary; LC, Lower Canning Estuary; UC, Upper Canning Estuary; CA = Canning Apex; LM, Lower Melville Water; MB, Matilda Bay; UM, Upper Melville Water; MC = Middle Canning Estuary.

Table 6. Mean squares (MS), percentage contribution of mean squares to the total mean squares (%MS) and significance levels (*P*) from pairwise PERMANOVA tests on the density of *Penaeus latisulcatus* 500 m^{-2} in nearshore waters of the Swan-Canning Estuary , over the breeding periods of October to March in 2013/14 to 2017/18, among (a) years and (b) subregions and in offshore waters of the same estuary among (c) years (d) months and (e) subregions. Non-significant results shaded in grey and the extent of significant difference denoted in superscript, ^{3} = $P < 0.05$, ^{2} = $P < 0.01$ and ^{1}= $P < 0.001$. EC = Entrance Channel; NM = North Melville Water; SM = South Melville Water; MS, Middle Swan Estuary; LC, Lower Canning Estuary; UC, Upper Canning Estuary; CA = Canning Apex; LM, Lower Melville Water; MB, Matilda Bay; UM, Upper Melville Water; MC = Middle Canning Estuary.

Nearshore waters

(a) Year	**13/14**	**14/15**	**15/16**	**16/17**
14/15	3.42^{1}			
15/16	1.94^{3}	1.26		
16/17	3.22^{2}	0.02	1.18	
17/18	2.23^{3}	4.35^{1}	3.49^{1}	4.26^{1}

(b) Subregion	**EC**	**NM**	**SM**	**PW**	**MS**	**LC**	**MC**	**UC**
NM	4.33^{1}							
SM	3.82^{1}							
PW	6.43^{1}	4.45^{1}	3.03^{1}					
MS	7.06^{1}	5.64^{1}	3.82^{1}	3.98^{1}				
LC	6.78^{1}	5.10^{1}	3.45^{2}	1.87	3.50^{1}			
MC	6.68^{1}	4.92^{1}	3.33^{2}	1.29	4.26^{1}	0.79		
UC	6.97^{1}	5.47^{1}	3.70^{1}	3.27^{1}	2.61^{2}	2.13^{3}	2.96^{2}	
CA	7.04^{1}	5.61^{1}	3.79^{1}	3.83^{1}	1.00	3.18^{2}	3.96^{1}	1.85

Offshore waters

(c) Year	**13/14**	**14/15**	**15/16**	**16/17**
14/15	5.61^{1}			
15/16	2.62^{2}	3.32^{2}		
16/17	0.91	1.49	0.39	
17/18	2.17^{3}	4.66^{1}	0.67	0.12

(d) Month	**Oct**	**Nov**	**Dec**	**Jan**	**Feb**
Nov	1.50				
Dec	2.53^{2}	0.93			
Jan	0.25	1.65	2.59^{2}		
Feb	1.78	2.21^{2}	2.44^{2}	1.69	
Mar	2.06^{3}	3.52^{1}	4.59^{1}	1.73	1.08

(e) Subregion	**EC**	**LM**	**MB**	**UM**	**PW**	**MS**	**LC**
LM	1.82						
MB	2.23^{2}	8.08^{1}					
UM	2.23^{2}	8.13^{1}					
PW	2.29^{2}	8.16^{1}	0.38	0.41			
MS	2.61^{1}	8.96^{1}	3.47^{1}	4.15^{1}	2.72^{3}		
LC	2.57^{2}	8.85^{1}	2.92^{2}	3.44^{1}	2.23^{3}	1.63	
MC	2.34^{2}	8.32^{1}	0.76	0.83	0.32	2.79^{2}	2.18^{3}

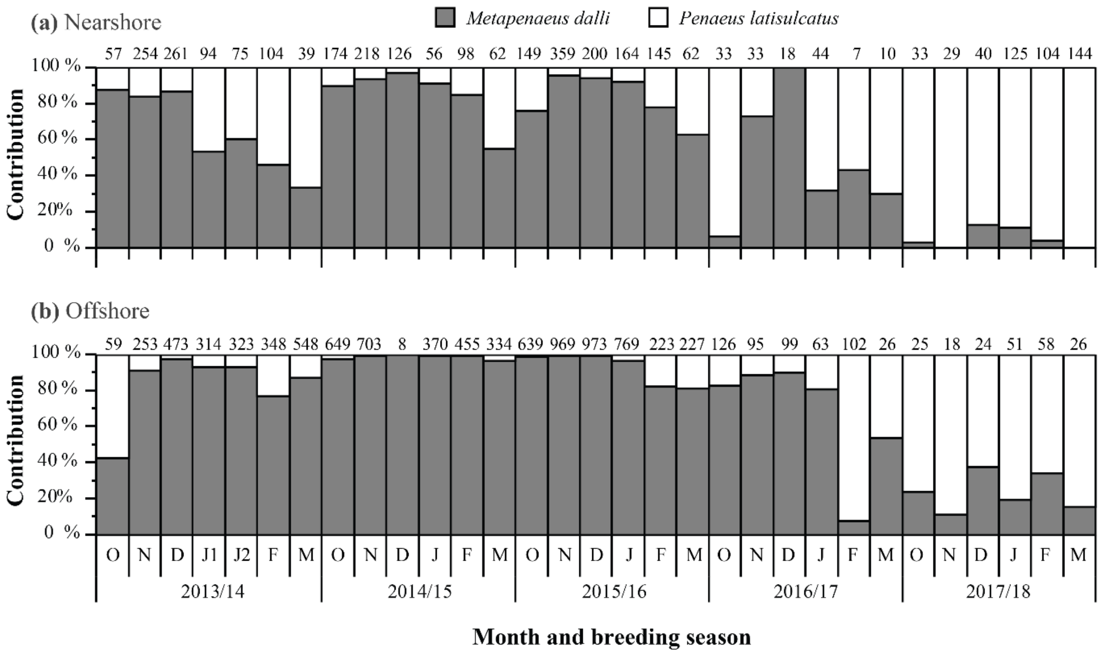

Fig. 19. Stacked bar graph of the total number of (■) *Metapenaeus dalli* and (☐) *Penaeus latisulcatus* collected from the (a) nearshore and (b) offshore waters of the Swan-Canning Estuary between each lunar month between October and March of the years between 2013/14 and 2017/18. The number of individuals recorded in each month are given above the stacked bar. Note two lunar months occurred in the calendar month of January 2014 and no data were obtained from some offshore sites in December 2014 due to a boat malfunction.

The contribution of *M. dalli* to the total prawn population was only 6% in October 2016 compared to an average value of 84% in the preceding three breeding seasons, after which the proportion of this species increased (*i.e.* 73 and 100% in November and December, respectively), before declining to ~30-40% for the remaining months of that breeding season (Fig. 19a). In 2017/18 however, *Penaeus latisulcatus* dominated the proportion of penaeids in all months, contributing at least 87% to the total numbers of prawns in each month. Furthermore, in marked contrast to all other years, no *M. dalli* were recorded in November or March of the 2017/18 breeding season.

Metapenaeus dalli comprised, on average, 90% of the penaeid fauna in the offshore waters of the Swan-Canning Estuary between October 2013 and January 2017 (Fig. 19b). Thus, in contrast to the nearshore waters, the proportion of this species did not decline towards the end of each breeding season. There was, however, a marked reduction in the density of this species compared to *P. latisulcatus* after January 2017, with *M. dalli* representing, on average, only 25% of the prawn population and as little as 8% in February 2017.

Discussion

This study determined how the density and egg production of the Western School Prawn *Metapenaeus dalli* changed in the Swan-Canning Estuary over five years, covering three years in which a restocking program occurred, releasing ~4.65 million hatchery-reared post-larvae and two years when major environmental perturbations affected the estuary. The density of *M. dalli*, which, at this latitude, completes its life-cycle with the estuary, *i.e.* a solely estuarine species (Potter et al., 1989; Crisp et al., 2018b), was compared to that of the Western King Prawn *Penaeus latisulcatus*, which spawns in marine waters and whose juveniles recruit to estuaries for a period, *i.e.* a marine estuarine-opportunist species (Potter *et al.*, 1991). The climatic events in the last two years of the study were a cold winter in 2016 and aseasonal heavy rainfall in February 2017, causing extensive hypoxia. A second major, aseasonal rainfall event took place in January 2018, lowering salinities but not oxygen concentrations. Emphasis is placed on determining how the population of *M. dalli* changed over the five years and elucidating whether such events influenced the population.

Inter-annual changes in abundance and egg production

Possible influence of restocking

Densities and egg production of *M. dalli* in both the nearshore and offshore waters of the Swan-Canning Estuary increased successively during the first three years of the study. Between 2013/14 and 2015/16, nearshore and offshore waters recorded an 58 and 109% increase in the density of *M. dalli*, a 302 and 18% increase in the number of gravid prawns and 1,912 and 124% increase in egg production, respectively. These increases in density and egg production followed releases of 600,000 post-larval *M. dalli* in 2013/14 and 2 million in 2014/15.

It should be noted that while environmental conditions differed in each of the first three years, these changes were not dramatic and were due to fine-scale changes in the timing and magnitude of rainfall and thus freshwater discharge, salinity, temperature and oxygen concentrations (see Crisp *et al.*, 2018b for detailed discussion of changes in abundance of gravid prawns and subsequent egg production from 2013/14 to 2015/16). Moreover, water quality in these three years were generally good for *M. dalli* being warm, normoxic and with marine-like salinities, particularly compared with the major changes in the summers of 2016/17 and 2017/18 (see later).

Given the sequential increase in *M. dalli* density and estimated egg production, the increases in the number of hatchery-reared individuals released and the different, but albeit typical environment conditions, the large scale releases of post-larvae are thought to have had a positive influence on the *M. dalli* population in the Swan-Canning Estuary. However, it was not possible to definitively determine the extent of the increase directly related to the restocking as there was no way to identify the hatchery-reared individuals. This mirrors with situation with the stocking of 5.8 million post-larval *Penaeus plebejus* in Tabourie Lake and Wallagoot Lake in New South Wales, where increases in prawn abundance were also detected, but the influence of the releases was not able to be quantified (Becker *et al.*, 2018).

Influence of climatic events on prawn numbers and egg production

Given the relatively large size of the *M. dalli* population and egg production in 2015/16 it was surprising that densities in both water depths in 2016/17 decreased by > 90%, and egg production by 85%, compared to 2013/14. This may reflect the atypically low air and water temperatures that occurred during winter of 2016 and persisted through spring. *Metapenaeus dalli* is a subtropical species, whose Australian distribution extends from Darwin in the north-east, along the western coast of Australia to the Peel-Harvey Estuary in south-western Australia (Grey et al., 1983; Potter et al., 1989). While throughout most of its range it occurs in shallow, inshore, marine waters (< 30 m deep), in latitudes south of 31°S it is confined to estuaries, which may reflect the fact that these systems maintain a higher water temperature during winter. In fact, individuals move from nearshore to offshore waters during winter, as these deeper waters are warmer (Poh et al., 2019) and their growth slows markedly, virtually ceasing (Broadley *et al.*, 2017). Moreover, being confined to the Swan-Canning Estuary and located towards the poleward limit of its range individuals would not be able to migrate away from the estuary into warmer waters. The cooler than average temperature in 2016/17, combined with hypoxic conditions in the Middle Swan Estuary between April and June 2016, a key area of the system at this time of year, probably thus resulted in direct mortality and also reduced the period of the year when individuals could grow. As a result, those that survive the cooler conditions would be of a smaller size and thus more vulnerable to predation. Post-larval *M. dalli* in the Swan-Canning Estuary were found to be eaten by a range of fishes, most notably the apogonid *Ostorhinchus rueppellii* and the atherinid *Atherinomorus vaigiensis* (Poh et al., 2018). As the spatio-temporal distributions of these teleosts overlap substantially with *M. dalli*, this penaeid does not have a spatial refuge from predation during any time of the year (Poh et al., 2019). Large prawns, however, would be less likely to be consumed by gape-limited predators. They also possess a greater tail-flip response (Arnott *et al.*, 1998; Guerin and Neil, 2015) and so are potentially better able to avoid predation by small-bodied teleosts, compared to smaller prawns.

The loss of individuals over winter, often referred to as overwintering mortality, has been recorded in a range of species and the effects of which are most pronounced for populations near the limits of its range (Thieltges *et al.*, 2004; Hurst, 2007; Ellis *et al.*, 2017). An analogous situation to *M. dalli* in the Swan-Canning Estuary is that of the portunid *Callinectes sapidus* in Chesapeake Bay, which, despite having tropical origins, is found in many temperate estuaries (Rome *et al.*, 2005). Egg production and brooding in this crab occur in the warmer months, with feeding, movement, growth and moulting all ceasing below 10 ºC (Hines *et al.*, 2010). Winter morality rates were typically < 3% during winters when bottom water temperature in February was at or above the 8-year average, but rose to 6.0–14.5% in cooler years (Rome *et al.*, 2005). Furthermore, during severe winters in Chesapeake Bay, such as 1996, the average overwintering survival was estimated to be only 30% (Bauer and Miller, 2010b). Mortality was not evenly spread across the size range with large crabs, and particularly females, suffering greater mortality (Rome *et al.*, 2005). For example, Sharov *et al.* (2003) estimated that the overall winter mortality was 11.9%, but was as high as 56.5% for crabs > 120 mm carapace width. If the same was true for *M. dalli* in the Swan-Canning Estuary, it would dramatically influence egg production in the early part of the breeding season, as it is the small population of large females that survive spawning and live for a second year that constitute the majority of the breeding cohort between October and December (Broadley *et al.*, 2017; Crisp *et al.*, 2018b).

Interestingly, Bauer and Miller (2010a) found that hatchery-raised *C. sapidus* experienced significantly lower survivorship than wild-caught individuals, and that small juveniles are more at risk of dying during the winter than larger juveniles. It is thus relevant that in 2015/16, 48% of the estimated egg production by *M. dalli* in nearshore waters, which was 20 times greater than in 2013/14, occurred in February and March. The larvae resulting from this late spawning would be substantially smaller during winter than individuals spawned earlier in the breeding season (Broadley *et al.*, 2017).

The lower abundances, delayed maturity and typically smaller size of *M. dalli* reduced egg production at the start of the 2016/17 breeding season. Moreover, in February 2017, when some of those individuals would have attained sexual maturity and spawned, an aseasonal rainfall event occurred, leading to marked increases in freshwater discharge, water column stratification and hypoxia. This occurred mainly in the Lower Canning Estuary and Melville Water (Trayler *et al.*, 2017), which, at this time of year, harbour large numbers of *M. dalli* in both water depths. Crustaceans are regarded as being typically sensitive to hypoxia (Vaquer-Sunyer and Duarte, 2008; Steckbauer *et al.*, 2011; Tweedley *et al.*, 2012). For example, no species of crustaceans were recorded for three months in the upper reaches of the Swan-Canning Estuary following a sustained period of hypoxia in 2010 (Tweedley *et al.*, 2016a). Poh et al. (2019) detected hypoxia (*i.e.* < 2 mgL^{-1}) and anoxia (*i.e.* < 0.5 mgL^{-1}) 47 and 21 times in 416 spot measurements of dissolved oxygen concentrations at the bottom of the water column when sampling for *M. dalli* in the Swan-Canning Estuary, between October 2013 and September 2015. During these times, densities of *M. dalli* in offshore waters were reduced or zero and, larger than 'normal' densities were recorded in corresponding nearshore waters, which were always normoxic (*i.e.* > 2 mgL^{-1}). This suggests that, in the event of localised hypoxia in deeper water, *M. dalli* move onshore, which conforms with an laboratory study on the congener *Metapenaeus ensis* demonstrating this penaeid can detect and avoid areas of hypoxia (Wu *et al.*, 2002).

Although *M. dalli* are able to move away from localised areas of hypoxia, the large spatial extent of low oxygen concentration, *i.e.* considerable portions of the Lower Canning Estuary and Melville Water (Trayler *et al.*, 2017), may have prevented their 'escape' to normoxic areas. In the nearby Peel-Harvey Estuary, blooms of the cynobacteria *Nodularia spumigena* resulted in mortalities among the less mobile bottom-living fishes and also crabs, whereas the more active species were able to migrate into other parts of the system and survive (Potter *et al.*, 1983; Steckis *et al.*, 1995). Mortality due to hypoxia thus likely explains the very low numbers of *M. dalli* caught in the remaining two months of the 2016/17 breeding season when no gravid females were caught (*i.e.* egg production = zero). The dramatic reduction in stock of *M. dalli* and cessation of spawning is thought to be responsible for the even fewer prawns collected in 2017/18 (*i.e.* only 4 and 3% of the 2013/14 population in the nearshore and offshore waters, respectively).

In contrast to the increase and subsequent dramatic decrease in the abundance of *M. dalli,* densities of the co-occurring *P. latisulcatus* remained relatively consistent over the five years of the study and even increased significantly in the nearshore waters in 2017/18 compared with 2013/14. These marked differences between *M. dalli* and *P. latisulcatus* were likely caused by the fact that i) no hatchery-reared *P. latisulcatus* were released, ii) *P. latisulcatus* is found throughout tropical and temperate Australia (Grey *et al.*, 1983) and thus is more tolerant of cooler temperatures, iii) *P. latisulcatus* occurs in further downstream areas of the estuary which did not experience pronounced hypoxia following the aseasonal heavy rainfall event and iv) *P. latisulcatus* is a marine estuarine-opportunist and as the adults spawn in coastal waters with juveniles recruiting to the estuary, recruitment can occur from outside populations even if the estuarine population suffers extinction (Penn, 1980; Potter *et al.*, 1991; Trayler *et al.*, 2017).

Spatial differences in abundance and egg production

The penaeids *M. dalli* and *P. latisulcatus* occurred in different areas of the system. Catches of *M. dalli* were greatest in the Middle Swan and Lower Canning Estuary, whereas densities of *P. latisulcatus* were largest at sites in Lower Melville Water and declined progressively in an upstream direction. The presence of *M. dalli*, a solely estuarine species, in the middle and upper reaches of the estuary reflects the fact that *M. dalli* is euryhaline and has been caught in salinities as low as 0.9 and 3.8 in nearshore and offshore waters, respectively in this system (Poh et al., 2019). Conversely, the marine spawning *P. latisulcatus*, was not recorded in salinities below 26 and was mainly restricted to the lower reaches of the system and particularly in offshore waters, mirroring its distribution in the Peel-Harvey Estuary (Potter et al., 1991; Poh et al., 2019). This pattern of spatial separation between metapenaeids and penaeids parallels the distribution patterns of *Metapenaeus macleayi* and *Penaeus plebejus* in the Hunter River Estuary, where juvenile *M. macleayi* extend into more upstream areas with variable salinities, while *P. plebejus* are restricted to the lower estuary (Taylor *et al.*, 2016; 2017b). In both cases, spatial separation is likely a mechanism to reduce potential competition (Ross, 1986).

Gravid *M. dalli* undergo a migration from the 'safety' of the deeper, offshore waters into shallow, nearshore areas to spawn, at which point they are exposed to being caught by recreational fishers. A number of key sites were identified that yielded large numbers of eggs and thus are important spawning areas for *M. dalli,* namely Canning Bridge and Deep Water Point in the Lower Canning Estuary and Maylands and Garrett Road Bridge in the Middle Swan Estuary. Typically, spawning occurs first in the Lower Canning Estuary, before moving upstream to the Middle Swan Estuary later in the season. This is likely due to the Canning River receiving less freshwater discharge than the Swan and the presence of a weir on the Canning, so that the Canning Estuary has more stable salinities earlier in the breeding season (Crisp *et al.*, 2018b). As the breeding season progresses, the salt wedge pushes further upstream, resulting in salinities in Lower and Upper Melville Water and the Lower Canning Estuary exceeding 35, whereas those in the Middle Swan Estuary are slightly reduced (*i.e.* 30-33 in 2013/14 to 2015/16; years without summer rainfall), which may favour the breeding success of this estuarine spawning species.

Conclusion and implications for future restocking

On the basis of the data obtained during this five-year study, the abundance of *M. dalli* in 2017/18 was the lowest recorded, being only 4 and 3% of catches in nearshore and offshore waters, respectively, of those in 2013/14. Thus, despite 240 hand trawls and 192 otter trawls being conducted in 2017/18, only 24 and 51 *M. dalli* were recorded, respectively. As it stands, the population of *M. dalli* in the Swan-Canning Estuary is extremely low.

This raises the question as to whether, if funds were available, restocking could be used to increase the abundance of this species. In order to minimise any genetic risks to the wild population of *M. dalli*, the restocking program collected gravid individuals using citizen scientists, informed by a scientific monitoring program (Jenkins et al., 2017; Tweedley et al., 2017b). This resulted in the collection of between 436 and 764 gravid females each year, which were used to produce 600,000 to 2,000,000 post-larvae. During our intensive sampling across both water depths in 2017/18, a total of only nine gravid individuals were recorded, compared to a range of 268 to 466 during the first three years of the study. Given the very low abundance of gravid *M. dalli* it may be difficult, and thus costly, to obtain sufficient quantities of eggs in order to undertake any restocking in the near future. However, if natural recruitment increased the population to the point where adequate numbers of gravid *M. dalli* were able to be collected in future years, restocking could then be used as a tool to increase the abundance of this iconic species, but this should be used in conjunction with traditional fisheries management measures.

Following discussions with DPIRD, DBCA, Recfishwest and some avid and experienced recreational fishers, a suite of recommendations for changes to the recreational fishery regulations were made by Tweedley et al. (2017a). These recommendations included: i) reduce the daily bag limit from 9L to 5L per person (noting it takes two people to operate a hand trawl net); ii) introduce a partial closure to hand trawling between 15 October to 15 December inclusive, to protect the gravid females spawning in the nearshore waters; iii) continue the existing fishing zone restrictions in relation to throw and hand trawl nets; iv) continue existing gear prescriptions and requirements to return by-catch to the water and v) develop a code of conduct to raise community awareness about sustainable fishing practices, *i.e.* release of female and, in particular, gravid prawns. Those recommendations are still relevant in 2019 for reducing any potential impacts of fishing on the stocks and allowing a proportion of mature individuals to spawn. However, given the very low abundance of *M. dalli* in the last two years consideration should also be given to more extensive closure periods and zonal restrictions.

If restocking is implemented in the future, its effectiveness should be monitored by a sampling regime similar to that in the current study, but the released prawns should also be marked using a genetic marker. As mentioned earlier it is not possible to distinguish wild and hatchery-reared *M. dalli* and, because of the small size at release and moulting of crustaceans, it is not possible to use physical tags to determine recapture rates of stocked prawns. Genetic markers *i.e.* allozymes, mitochondrial DNA, RFLP, RAPD, AFLP, microsatellite, SNP, and EST markers, provide a potential method to distinguish stocked from wild individuals (Bravington and Ward, 2004) and have been developed to some extent for *Penaeus japonicus*, *Penaeus esculentus* and *Penaeus plebejus* (Jerry *et al.*, 2004; Liu and Cordes, 2004; Loneragan *et al.*, 2004; Chan *et al.*, 2014) and proven successful for the Blue Crab in North America *Callinectes sapidus* (Feng *et al.*, 2017). However, a greater number of markers would be needed for *M. dalli* than the above three *Penaeus* species, as the current culture practice for *M. dalli* involves collecting wild broodstock and therefore, the genotypes of the fathers of the hatchery-reared prawns are not known. Currently, research is progressing to identify possible genetic markers using microsatellites as part of the PhD research by Brian Poh at Murdoch University.

References

Anderson, D.M., Burkholder, J.M., Cochlan, W.P., Glibert, P.M., Gobler, C.J., Heil, C.A., Kudela, R.M., Parsons, M.L., Rensel, J.E.J., Townsend, D.W., Trainer, V.L., Vargo, G.A., 2008a. Harmful algal blooms and eutrophication: Examining linkages from selected coastal regions of the United States. Harmful Algae 8, 39-53.

Anderson, M.J., Gorley, R.N., Clarke, K.R., 2008b. PERMANOVA+ for PRIMER: guide to software and statistical methods. PRIMER-E, Plymouth, UK.

Arlinghaus, R., Mehner, T., 2005. Determinants of management preferences of recreational anglers in Germany: Habitat management versus fish stocking. Limnologica - Ecology and Management of Inland Waters 35, 2-17.

Arlinghaus, R., Beardmore, B., Riepe, C., Meyerhoff, J., Pagel, T., 2014. Species-specific preferences of German recreational anglers for freshwater fishing experiences, with emphasis on the intrinsic utilities of fish stocking and wild fishes. Journal of Fish Biology 85, 1843-1867.

Arnott, S., Neil, D., Ansell, A., 1998. Tail-flip mechanism and size-dependent kinematics of escape swimming in the brown shrimp *Crangon crangon*. Journal of Experimental Biology 201, 1771-1784.

Australian Bureau of Statistics, 2015. Australian Demographic Statistics.

Bartley, D.M., De Graaf, G.J., Valbo-Jørgensen, J., Marmulla, G., 2015. Inland capture fisheries: status and data issues. Fisheries Management and Ecology 22, 71-77.

Bauer, L.J., Miller, T.J., 2010a. Temperature-, salinity-, and size-dependent winter mortality of juvenile Blue Crabs (*Callinectes sapidus*). Estuaries and Coasts 33, 668-677.

Bauer, L.J., Miller, T.J., 2010b. Spatial and interannual variability in winter mortality of the Blue Crab (*Callinectes sapidus*) in the Chesapeake Bay. Estuaries and Coasts 33, 678-687.

Becker, A., Lowry, M.B., Taylor, M.D., 2018. Response of estuarine consumer communities following the stocking of a juvenile penaeid (*Penaeus plebejus*) over two consecutive years. Fisheries Management and Ecology 25, 54-65.

Bell, J.D., Rothlisberg, P.C., Munro, J.L., Loneragan, N.R., Nash, W.J., Ward, R.D., Andrew, N.R., 2005. Restocking and stock enhancement of marine invertebrate fisheries. Advances in Marine Biology 49, 1-374.

Blankenship, H.L., Leber, K.M., 1995. A responsible approach to marine stock enhancement. American Fisheries Society Symposium 15, 167-175.

Blount, C., O'Donnell, P., Reeds, K., Taylor, M.D., Boyd, S., Van derWalt, B., McPhee, D.P., Lincoln Smith, M., 2017. Tools and criteria for ensuring estuarine stock enhancement programs maximise benefits and minimise impacts. Fisheries Research 186, 413-425.

Born, A.F., Immink, A.J., Bartley, D.M., 2004. Marine and coastal stocking: global status and information needs, in: Bartley, D.M., Leber, K.M. (Eds.), FAO Fisheries Technical Paper 429, Marine ranching. FAO, Rome, pp. 1-12.

Bravington, M., Ward, R., 2004. Microsatellite DNA markers: evaluating their potential for estimating the proportion of hatchery-reared offspring in a stock enhancement programme Molecular Ecology 13, 1287-1297.

Brearley, A., 2005. Ernest Hodgkin's Swanland, 1st ed. University of Western Australia Press, Crawley.

Broadley, A.D., Tweedley, J.R., Loneragan, N.R., 2017. Estimating biological parameters for penaeid restocking in a temperate Australian estuary. Fisheries Research 186, 488-501.

Chan, J.T., Sherwin, W.B., Taylor, M.D., 2014. A tool for tracking genetic contributions of wild *Penaeus* (*Melicertus*) *plebejus* broodstock to hatchery populations. Animal genetics 45, 888-892.

Cottingham, A., Hall, N.G., Potter, I.C., 2015. Performance and contribution to commercial catches and egg production by restocked *Acanthopagrus butcheri* (Sparidae) in an estuary. Estuarine, Coastal and Shelf Science 164, 194-203.

Creighton, C., Boon, P.I., Brookes, J.D., Sheaves, M., 2015. Repairing Australia's estuaries for improved fisheries production – what benefits, at what cost? Marine and Freshwater Research 66, 493-507.

Crisp, J.A., Tweedley, J.R., D'Souza, F.M., Partridge, G.J., Moheimani, N.R., 2016. Larval development of the western school prawn *Metapenaeus dalli* Racek, 1957 (Crustacea: Decapoda: Penaeidae) reared in the laboratory. Journal of Natural History 50, 1699-1724.

Crisp, J.A., D'Souza, F.M.L., Tweedley, J.R., Partridge, G.J., Moheimani, N.R., 2017a. Performance of mixed species and mono-specific algal diets for culture of larval Western School Prawns, *Metapenaeus dalli*. Journal of the World Aquaculture Society.

Crisp, J.A., D’Souza, F.M.L., Tweedley, J.R., Partridge, G.J., Moheimani, N.R., 2017b. Quantitative determination of ovarian development in penaeid prawns (Decapoda: Penaeidae). Journal of Crustacean Biology 37, 81-89.

Crisp, J.A., Partridge, G.J., D’Souza, F.M.L., Tweedley, J.R., Moheimani, N.R., 2017c. Effects of temperature and salinity on larval survival and development of the western school prawn *Metapenaeus dalli*. International Aquatic Research 9, 1-10.

Crisp, J.A., D'Souza, F.M.L., Tweedley, J.R., Partridge, G.J., Moheimani, N.R., 2018a. Performance of mixed species and mono-specific algal diets for culture of larval Western School Prawns, *Metapenaeus dalli*. Journal of the World Aquaculture Society 49, 845-856.

Crisp, J.A., Loneragan, N.R., Tweedley, J.R., D'Souza, F.M.L., Poh, B., 2018b. Environmental factors influencing the reproduction of an estuarine penaeid population and implications for management. Fisheries Management and Ecology 25, 203-219.

Davis, J.R., Koop, K., 2006. Eutrophication in Australian rivers reservoirs and estuaries - a southern hemisphere perspective on the science and its implications. Hydrobiologia 559, 23-76.

De Grave, S., 2014. *Metapenaeus* Wood-Mason in Wood-Mason & Alcock, 1891a. World Register of Marine Species.

Dichmont, C.M., Deng, A.R., Punt, A.E., Venables, W., Haddon, M., 2006. Management strategies for short lived species: The case of Australia's Northern Prawn Fishery: 3. Factors affecting management and estimation performance. Fisheries Research 82, 235-245.

Ellis, T.A., Buckel, J.A., Hightower, J.E., 2017. Winter severity influences spotted seatrout mortality in a southeast US estuarine system. Marine Ecology Progress Series 564, 145-161.

Feng, X., Johnson, E.G., Williams, E.P., Place, A.R., 2017. Successful identification and discrimination of hatchery-reared Blue Crabs (*Callinectes sapidus*) released into the Chesapeake Bay using a genetic tag. Journal of Shellfish Research 36, 277-282.

Garlock, T.M., Camp, E.V., Lorenzen, K., 2017. Using fisheries modeling to assess candidate species for marine fisheries enhancement. Fisheries Research 186, 460-467.

Garlock, T.M., Lorenzen, K., 2017. Marine angler characteristics and attitudes toward stock enhancement in Florida. Fisheries Research 186, 439-445.

Gentilli, J., 1971. World Survey of Climatology. Volume 13. Climate of Australia and New Zealand. Elsevier Publishing Company., Amsterdam.

Grey, D.L., Dall, W., Baker, A., 1983. A Guide to the Australian Penaeid Prawns, A guide to the Australian penaeid prawns. Northern Territory Government Printing Office, Darwin, Australia, p. 140.

Guerin, A.J., Neil, D.M., 2015. Escape trajectories of the Rockpool Prawn (*Palaemon elegans*) in response to visual and mechanosensory stimuli. Marine and Freshwater Behaviour and Physiology 48, 145-161.

Hallett, C.S., Hobday, A.J., Tweedley, J.R., Thompson, P.A., McMahon, K., Valesini, F.J., 2018. Observed and predicted impacts of climate change on the estuaries of south-western Australia, a Mediterranean climate region. Regional Environmental Change 18, 1357-1373.

Hilborn, R., 1998. The economic performance of marine stock enhancement projects. Bulletin of Marine Science 62, 661-674.

Hines, A.H., Johnson, E.G., Darnell, M.Z., Rittschof, D., Miller, T.J., Bauer, L.J., Rodgers, P., Aguilar, R., 2010. Predicting effects of climate change on blue crabs in Chesapeake Bay, in: Kruse, G.H., Eckert, G.L., Foy, R.J., Lipcius, R.N., Sainte-Marie, B., Stram, D.L., Woodby, D. (Eds.), Biology and Management of Exploited Crab Populations Under Climate Change. Alaska Sea Grant, University of Alaska Fairbanks, pp. 109-127.

Hodgkin, E.P., Hesp, P., 1998. Estuaries to salt lakes: Holocene transformation of the estuarine ecosystems of south-western Australia. Marine and Freshwater Research 49, 183-201.

Hoeksema, S.D., Chuwen, B.M., Tweedley, J.R., Potter, I.C., 2018. Factors influencing marked variations in the frequency and timing of bar breaching and salinity and oxygen regimes among normally-closed estuaries. Estuarine, Coastal and Shelf Science 208, 205-218.

Hurst, T.P., 2007. Causes and consequences of winter mortality in fishes. Journal of Fish Biology 71, 315-345.

Ingram, B.A., De Silva, S.S., 2015. General aspects of stock enhancement in fisheries developments. , in: De Silva, S.S., Ingram, B.A., Wilkinson, S. (Eds.), Perspectives on culture-based fisheries developments in Asia. Network of Aquaculture Centres in Asia-Pacific Bangkok, Thailand., pp. 27-37.

Jenkins, G.I., Tweedley, J.R., Trayler, K.M., 2017. Re-establishing recreational prawning in the Swan-Canning Estuary. Western Australian Fish Foundation, Perth, Western Australia, p. 128.

Jerry, D.R., Preston, N.P., Crocos, P.J., Keys, S.J., Meadows, J.R.S., Li, Y., 2004. Parentage determination of Kuruma Shrimp *Penaeus* (*Marsupenaeus*) *japonicus* using microsatellite markers (Bate). Aquaculture 235, 237-247.

Kitada, S., Kishino, H., 2006. Lessons learned from Japanese marine finfish stock enhancement programmes. Fisheries Research 80, 101-112.

Kitada, S., Shishidou, H., Sugaya, T., Kitakado, T., Hamasaki, K., Kishino, H., 2009. Genetic effects of long-term stock enhancement programs. Aquaculture 290, 69-79.

Kitada, S., 2018. Economic, ecological and genetic impacts of marine stock enhancement and sea ranching: A systematic review. Fish and Fisheries 19, 511-532.

Kompas, T., Dichmont, C.M., Punt, A.E., Deng, A., Che, T.N., Bishop, J., Gooday, P., Ye, Y., Zhou, S., 2010. Maximizing profits and conserving stocks in the Australian Northern Prawn Fishery. Australian Journal of Agricultural and Resource Economics 54, 281-299.

Levin, P.S., Zabel, R.W., Williams, J.G., 2001. The road to extinction is paved with good intentions: negative association of fish hatcheries with threatened salmon. Proceedings of the Royal Society of London. Series B: Biological Sciences 268, 1153-1158.

Liu, Z.J., Cordes, J., 2004. DNA marker technologies and their applications in aquaculture genetics. Aquaculture 238, 1-37.

Loneragan, N.R., Crocos, P.J., Barnard, R., McCulloch, R., Penn, J.W., Ward, R.D., Rothlisberg, P.C., 2004. An approach to evaluating the potential for stock enhancement of Brown Tiger Prawns (*Penaeus esculentus* Haswell) in Exmouth Gulf, Western Australia, in: Leber, K.M., Kitada, S., Blankenship, H.L., Svasand, T. (Eds.), Stock

Enhancement and Sea Ranching: Developments, Pitfalls and Opportunities, 2nd Edition. Wiley-Blackwell, Oxford, UK, pp. 444-464.
Loneragan, N.R., Jenkins, G.I., Taylor, M.D., 2013. Marine stock enhancement, restocking and sea ranching in Australia: future directions and a synthesis of two decades of research and development. Reviews in Fisheries Science 21, 222-236.
Lorenzen, K., Amarasinghe, U.S., Bartley, D.M., Bell, J.D., Bilio, M., De Silva, S.S., Garaway, C.J., Hartmann, W.D., Kapetsky, J.M., Laleye, P., Moreau, J., Sugunan, V.V., Swar, D.B., 2000. Strategic review of enhancements and culture-based fisheries, Technical Proceedings of the Conference on Aquaculture in the Third Millennium. Network of Aquaculture Centres in Asia-Pacific, Bangkok, Thailand, pp. 221-237.
Lorenzen, K., 2005. Population dynamics and potential of fisheries stock enhancement: practical theory for assessment and policy analysis. Philosophical Transactions of the Royal Society B: Biological Sciences 360, 171.
Lorenzen, K., Leber, K.M., Blankenship, H.L., 2010. Responsible approach to marine stock enhancement: an update. Reviews in Fisheries Science 18, 189-210.
Lorenzen, K., Agnalt, A.-L., Blankenship, H.L., Hines, A.H., Leber, K.M., Loneragan, N.R., Taylor, M.D., 2013. Evolving context and maturing science: aquaculture-based enhancement and restoration enter the marine fisheries management toolbox. Reviews in Fisheries Science 21, 213-221.
Maher, J., 2002. Where have all the Swan-Canning prawns gone. Western Fisheries 2002, 20-21.
Malseed, B.E., Sumner, N.R., 2001. A 12-month survey of recreational fishing in the Swan-Canning Estuary Basin of Western Australia during 1998-99. Department of Fisheries, Western Australia, Perth, Australia, p. 44.
Montgomery, S.S., 2010. Biology and Life Cycles of Prawns. New South Wales Department of Primary Industrie, Orange, Australia.
Obregón, C., Hughes, M., Loneragan, N.R., Poulton, S.J., Tweedley, J.R., in press. Good crab, bad crab: recreational fishers supportive and aware of trade-offs associated with restocking. Ambio.
Partridge, G.J., Ginbey, B.M., Woolley, L.D., Fairclough, D.V., Crisafulli, B., Chaplin, J., Prokop, N., Dias, J., Bertram, A., Jenkins, G.I., 2017. Development of techniques for the collection and culture of wild-caught fertilised snapper (Chrysophrys auratus) eggs for stock enhancement purposes. Fisheries Research 186, 524-530.
Penn, J.W., 1980. Spawning and fecundity of the Western King Prawn, *Penaeus latisulcatus* Kishinouye, in western Australian waters. Marine and Freshwater Research 31, 21-35.
Poh, B., Tweedley, J.R., Chaplin, J.A., Trayler, K.M., Loneragan, N.R., 2018. Estimating predation rates of restocked individuals: The influence of timing-of-release on metapenaeid survival. Fisheries Research 198, 165-179.
Poh, B., Tweedley, J.R., Chaplin, J.A., Trayler, K.M., J.A., C., Loneragan, N.R., 2019. Influence of physico-chemical and biotic factors on the distribution of a penaeid in a temperate estuary. Estuarine, Coastal and Shelf Science 218, 70-85.
Potter, I.C., Loneragan, N.R., Lenanton, R.C.J., Chrystal, P.J., 1983. Blue-green algae and fish population changes in a eutrophic estuary. Marine Pollution Bulletin 14, 228-233.
Potter, I.C., Penn, J.W., Brooker, K.S., 1986. Life cycle of the Western School Prawn, *Metapenaeus dalli* Racek, in a Western Australian estuary. Marine and Freshwater Research 37, 95-103.
Potter, I.C., Baronie, F.M., Manning, R.J.G., Loneragan, N.R., 1989. Reproductive biology and growth of the western school prawn, *Metapenaeus dalli*, in a large Western Australian estuary. Australian Journal of Marine and Freshwater Research 40, 327-340.

Potter, I.C., Manning, R.J.G., Loneragan, N.R., 1991. Size, movements, distribution and gonadal stage of the Western King Prawn (*Penaeus latisulcatus*) in a temperate estuary and local marine waters. Journal of Zoology 223, 419-445.
Potter, I.C., Chuwen, B.M., Hesp, S.A., Hall, N.G., Hoeksema, S.D., Fairclough, D.V., Rodwell, T.M., 2011. Implications of the divergent use of a suite of estuaries by two exploited marine fish species. Journal of Fish Biology 79, 662-691.
Potter, I.C., Tweedley, J.R., Elliott, M., Whitfield, A.K., 2015a. The ways in which fish use estuaries: a refinement and expansion of the guild approach. Fish and Fisheries 16, 230-239.
Potter, I.C., Warwick, R.M., Hall, N.G., Tweedley, J.R., 2015b. The physico-chemical characteristics, biota and fisheries of estuaries, in: Craig, J. (Ed.), Freshwater Fisheries Ecology. Wiley-Blackwell, pp. 48-79.
Racek, A., 1957. Systematic position of the school prawn from Western Australia. Fisheries Bulletin, Western Australia 6, 1-13.
Rome, M.S., Young-Williams, A.C., Davis, G.R., Hines, A.H., 2005. Linking temperature and salinity tolerance to winter mortality of Chesapeake Bay blue crabs (*Callinectes sapidus*). Journal of Experimental Marine Biology and Ecology 319, 129-145.
Ross, S.T., 1986. Resource partitioning in fish assemblages: a review of field studies. Copeia, 352-388.
Ryan, K.L., Hall, N.G., Lai, E.K., Smallwood, C.B., Taylor, S.M., Wise, B.S., 2015. State-wide survey of boat-based recreational fishing in Western Australia 2013/14, Fisheries Research Report No. 268, Department of Fisheries, Western Australia, p. 208.
Sharov, A.F., Vølstad, J.H., Davis, G.R., Davis, B.K., Lipcius, R.N., Montane, M.M., 2003. Abundance and exploitation rate of the blue crab (*Callinectes sapidus*) in Chesapeake Bay. Bulletin of Marine Science 72, 543-565.
Smith, K., Lenanton, R., Valesini, F., 2007. Preliminary survey to determine the abundance of river prawns (*Metapenaeus dalli*) in the Swan-Canning Estuary. Department of Fisheries, Western Australia, Perth, Australia, p. 11.
Smith, K.A., 2006. Review of fishery resources and status of key fishery stocks in the Swan-Canning Estuary. Department of Fisheries, Western Australia, Perth, Australia, p. 86.
Smithwick, W., Reid, K., Ensor, R., 2011. Black Water Prawning: Drag Netting in the Swan River. Arts Naked Publications, Perth, Australia.
Steckbauer, A., Duarte, C.M., Carstensen, J., Vaquer-Sunyer, R., Conley, D.J., 2011. Ecosystem impacts of hypoxia: thresholds of hypoxia and pathways to recovery Environmental Research Letters 6, 025003.
Steckis, R.A., Potter, I.C., Lenanton, R.C.J., 1995. The commercial fisheries in three south-western Australian estuaries exposed to different degrees of eutrophication, in: McComb, A.J. (Ed.), Eutrophic Shallow Estuaries and Lagoons. CRC Press, Boca Raton, pp. 189-203.
Taylor, M.D., Palmer, P.J., Fielder, D.S., Suthers, I.M., 2005. Responsible estuarine finfish stock enhancement: an Australian perspective. Journal of Fish Biology 67, 299-331.
Taylor, M.D., Smith, J.A., Boys, C.A., Whitney, H., 2016. A rapid approach to evaluate putative nursery sites for penaeid prawns. Journal of Sea Research 114, 26-31.
Taylor, M.D., Chick, R.C., Lorenzen, K., Agnalt, A.-L., Leber, K.M., Blankenship, H.L., Haegen, G.V., Loneragan, N.R., 2017a. Fisheries enhancement and restoration in a changing world. Fisheries Research 186, Part 2, 407-412.
Taylor, M.D., Fry, B., Becker, A., Moltschaniwskyj, N., 2017b. The role of connectivity and physicochemical conditions in effective habitat of two exploited penaeid species. Ecological Indicators 80, 1-11.

Thieltges, D.W., Strasser, M., van Beusekom, J.E.E., Reise, K., 2004. Too cold to prosper—winter mortality prevents population increase of the introduced American slipper limpet *Crepidula fornicata* in northern Europe. Journal of Experimental Marine Biology and Ecology 311, 375-391.

Trayler, K.M., Cosgrove, J.J., Hoeksema, S.D., Hipsey, M.R., 2017. Flood 2017: Impacts on environmental and social values of an urban estuary, Australian Marine Science Conference 2017, Darwin, Australia.

Tweedley, J.R., Warwick, R.M., Valesini, F.J., Platell, M.E., Potter, I.C., 2012. The use of benthic macroinvertebrates to establish a benchmark for evaluating the environmental quality of microtidal, temperate southern hemisphere estuaries. Marine Pollution Bulletin 64, 1210-1221.

Tweedley, J.R., Warwick, R.M., Clarke, K.R., Potter, I.C., 2014. Family-level AMBI is valid for use in the north-eastern Atlantic but not for assessing the health of microtidal Australian estuaries. Estuarine, Coastal and Shelf Science 141, 85-96.

Tweedley, J.R., Hallett, C.S., Warwick, R.M., Clarke, K.R., Potter, I.C., 2016a. The hypoxia that developed in a microtidal estuary following an extreme storm produced dramatic changes in the benthos. Marine and Freshwater Research 67, 327-341.

Tweedley, J.R., Warwick, R.M., Potter, I.C., 2016b. The contrasting ecology of temperate macrotidal and microtidal estuaries. Oceanography and Marine Biology: An Annual Review 54, 73-171.

Tweedley, J.R., Loneragan, N.R., Crisp, J.A., Poh, B., Broadley, A.D., Bennett, A.L., Hodson, K.P., Trayler, K.M., Jenkins, G.I., Chaplin, J.A., 2017a. Stock enhancement of the Western School Prawn (*Metapenaeus dalli*) in the Swan-Canning Estuary; evaluating recruitment limitation, environment and release strategies. Report for the Fisheries Research and Development Corporation, Murdoch University, Perth, Western Australia, p. 546.

Tweedley, J.R., Loneragan, N.R., Crisp, J.A., Poh, B., Broadley, A.D., Bennett, A.L., Hodson, K.P., Trayler, K.M., Jenkins, G.I., Chaplin, J.A., 2017b. Restocking of the Western School Prawn (*Metapenaeus dalli*) in the Swan Canning Riverpark. Department of Parks and Wildlife, Murdoch University, Perth, Western Australia, p. 537.

Vaquer-Sunyer, R., Duarte, C.M., 2008. Thresholds of hypoxia for marine biodiversity. Proceedings of the National Academy of Sciences 105, 15452-15457.

Warwick, R.M., Clarke, K.R., 1993. Comparing the severity of disturbance: A meta-analysis of marine macrobenthic community data. Marine Ecology Progress Series 92, 221-231.

Warwick, R.M., Tweedley, J.R., Potter, I.C., 2018. Microtidal estuaries warrant special management measures that recognise their critical vulnerability to pollution and climate change. Marine Pollution Bulletin 135, 41-46.

Welcomme, R.L., Bartley, D.M., 1998. Current approaches to the enhancement of fisheries. Fisheries Management and Ecology 5, 351-382.

Wu, R.S.S., Lam, P.K.S., Wan, K.L., 2002. Tolerance to, and avoidance of, hypoxia by the penaeid shrimp (*Metapenaeus ensis*). Environmental Pollution 118, 351-355.

Zhang, J., Gilbert, D., Gooday, A., Levin, L., Naqvi, S., Middelburg, J., Scranton, M., Ekau, W., Pena, A., Dewitte, B., Oguz, T., Monteiro, P., Urban, E., Rabalais, N., Ittekkot, V., Kemp, W.M., Ulloa, O., Elmgren, R., Escobar-Briones, E., Van der Plas, A., 2010. Natural and human-induced hypoxia and consequences for coastal areas: synthesis and future development. Biogeosciences 7, 1443-1467.