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**Poh, B., Tweedley, J.R., Chaplin, J.A., Trayler, K.M. and Loneragan, N.R.  
(2017) Estimating predation rates of restocked individuals: The influence  
of timing-of-release on metapenaeid survival. Fisheries Research, In press.**

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# **Estimating predation rates of restocked individuals: the influence of timing-of-release on metapenaeid survival**

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## **Abstract**

The success of aquaculture-based enhancement programs is greatly influenced by the survival of released individuals. Immediate post-release mortality through predation is one of the greatest obstacles to the success of releases, and the choice of a release site or time-of-release can be critical in maximising survival. This paper develops a novel quantitative method of estimating predation rate to inform release programs, and describes its use in determining whether hatchery-reared Western School Prawns *Metapenaeus dalli* should be released into the Swan-Canning Estuary in temperate south-western Australia during the night or day. Fish faunal composition was determined during the day and night, both before and after the release of ~130,000 postlarval *M. dalli*. Far greater numbers of species and individuals were recorded at night. Stomach contents of 16 abundant teleost species were estimated volumetrically (%V) and any postlarval *M. dalli* counted. Although diet varied among species, diel phase and size class, crustaceans (including *M. dalli*) were a key dietary component (>10 %V) of 12 species. The data on the abundance of these fish species and the number of *M. dalli* they consumed were combined and subjected to bootstrapping, to estimate the total relative number of *M. dalli* consumed at the time-of-release. The results indicated that while six species consumed *M. dalli*, two species, *Ostorhinchus rueppellii* (Apogonidae) and *Atherinomorus vaigiensis* (Atherinidae), were responsible for ~99 % of the predation, and that the total number of postlarval prawns consumed was 288 % higher at night than in the day. These findings suggest that releasing *M. dalli* during the day will greatly reduce predation and consequently allow a greater survival rate at this release site. The simple methodology developed here could be readily employed to inform release strategies for other species.

**Keywords:** dietary composition; release program; release strategy; stock enhancement; survival.

## **Introduction**

Over the last thirty years, interest in aquaculture-based enhancement (i.e. release programs for cultured species) has increased greatly because of the potential for such programs to provide increased food security, socioeconomic benefits and/or restore populations subjected to anthropogenic stress (Taylor et al., 2017). These programs include stock enhancement, restocking and sea ranching (Bell et al., 2008; Lorenzen et al., 2013). Despite their obvious attraction as a mechanism to increase fisheries production and rebuild fish stocks, the performance of release programs has been mixed and, more often than not, disappointing, with many failing to significantly increase fishery yields or provide economic benefits (Bell et al., 2005; Lorenzen, 2005).

Predation is widely understood as a major contributing factor affecting the short-term post-release survival of hatchery-reared juveniles (Stein et al., 1981; Støttrup et al., 2008), and can contribute >95 % of total mortality (Hines et al., 2008). Predation is also considered a major cause of natural mortality in postlarval penaeids (Minello and Zimmerman, 1983; Zimmerman et al., 1984). Dall et al. (1990) suggested that 25 % of juvenile prawns in coastal inland waters are lost each week, mainly due to predation. This high level of natural mortality may be related to the high energy content of penaeids relative to other benthic macroinvertebrates, making them attractive prey (Thayer et al., 1973). Predation rates, and as a consequence natural mortality, of juvenile penaeids vary greatly among habitat types (Haywood et al., 1998; 2003; Kenyon et al., 1995), which influences the number of prawns surviving to migrate from juvenile habitats to recruit into fisheries (Loneragan et al., 2006; Ye et al., 2005).

Whilst the impact of fish predation on adult penaeids has been well studied (Pauly and Palomares, 1987; Salini et al., 1990; Sheridan et al., 1984), predation rates on juveniles in estuaries and coastal waters have received less attention. This is possibly because postlarval and juvenile penaeids are rapidly digested in fish stomachs, causing them to be under-represented in stomach content analyses; e.g. small penaeids were reduced to ~30 % of their

original dry weight just one hour after ingestion by the tetradontid *Monocanthus chinensis* (Haywood, 1995).

A study by Salini et al. (1990) found that 37 of the 77 fish species collected in the Embley Estuary fed on juvenile penaeids, which were a significant component of the diets of three of the most abundant predators. Numerous studies have found that many predatory fish are size selective; i.e. smaller fish eat smaller prey (Brewer et al., 1995; Lek et al., 2011), which is important for release programs as, typically, releases comprise a single size-class (cohort). Modelling estimated that the sources of greatest uncertainties in predicting the survival of Brown Tiger Prawns, *Penaeus esculentus*, following their release was in the immediate post-release mortality, natural mortality rates of the juvenile phase and density-dependent effects (Ye et al., 2005). Differences in 'fitness' have also been detected between hatchery-reared and wild postlarval penaeids. For example, Ochwada-Doyle et al. (2012), found that wild-caught Eastern King Prawn, *Penaeus (Melicertus) plebejus*, postlarvae out-competed hatchery-raised postlarvae for shelter, resulting in higher predation rates on the hatchery-raised individuals. Thus, in order to estimate the effect of predation on the success of release programs, studies must focus on the predation on a particular size-class(es), i.e. that of the hatchery-reared and released individuals.

The abundance of predators is a major contributing factor to predation pressure (Hereu et al., 2005). Ichthyofaunal assemblages in estuaries are very dynamic and can vary spatially, and over a range of temporal scales, e.g. seasons/years/decades (Potter et al., 2016; Ribeiro et al., 2008), seasons (Loneragan and Potter, 1990; Veale et al., 2014) and diel phase (Gray et al., 1998; Young et al., 1997). The production and release of hatchery-reared individuals that do not have cultured broodstock available, i.e. for species whose life cycle has not been closed, is limited by the temporal availability of wild broodstock. Release strategies are therefore constrained to controlling the site and time-of-day of release, but not season. Although diel changes in fish composition have been recorded in several estuaries in temperate southwestern Australia, with different species being more abundant at one time of day/night, the trends are not consistent across estuaries (c.f. Hoeksema and Potter, 2006; Yeoh et al., 2017).

Generalisations on the diel abundance of predators for the design of a release program are therefore difficult to make.

The dietary compositions of many fish species differ markedly over the diel cycle (Klumpff and Nichols, 1983; Linke et al., 2001; Robertson and Howard, 1978), which is often related to changes in the availability of prey species. The diets of fish species also vary significantly with ontogeny, switching from smaller to larger prey with increasing body size (Franco et al., 2008; Lek et al., 2011). Furthermore, Daly et al. (2013) highlighted the importance for investigating both spatial and temporal variation in predation pressure in their study on the stock enhancement of Red King Crab (*Paralithodes camtschaticus*). Thus, understanding the abundance, feeding habitats and dietary composition of predator species is vital when developing release strategies that minimise short-term post-release mortality.

The abundance of the Western School Prawn (*Metapenaeus dalli*), which was once the focus of a small commercial and iconic recreational fishery in the Swan-Canning Estuary, Western Australia, has declined markedly since the 1950s (Smith et al., 2007; Smith, 2006). Despite a large reduction in fishing pressure, stocks of *M. dalli* have not recovered, and thus a restocking project was initiated as a possible means of increasing the population size (Broadley et al., 2017). The overall aim of this study is to develop a quantitative method for estimating the immediate post-release effects of predation and determine whether releases of hatchery-reared postlarval *M. dalli* should be conducted during the day or night. In order to achieve this, we aimed to: (i) determine diel changes in the characteristics of the fish fauna at the release site in the Swan-Canning Estuary; (ii) quantify the dietary composition of abundant teleost species prior to and immediately after releases; and (iii) estimate the number of *M. dalli* consumed following releases during the day and night. The results provide the quantitative data required to develop a release strategy that optimises the immediate post-release survival of postlarval *M. dalli*.

## Materials and methods

### *Release of postlarval prawns*

In each of March 2015 and March 2016, a total of ~130,000 *M. dalli* postlarvae (PL12, ~4 mm total length [TL]) were released into Matilda Bay in the Swan-Canning Estuary (Fig. 1). The hatchery-reared PL12 prawns were fully metamorphosed, had adopted a benthic lifestyle, and were better able to shelter and avoid predators than the earlier pelagic nauplii, protozoal and mysis stages (Crisp et al., 2016; Dall et al., 1990). The postlarvae were grown at the Australian Centre for Applied Aquaculture Research from fertilised eggs released by approximately 40 gravid females collected from the wild (Jenkins et al., 2017).

In the hatchery, PL12s were collected from 300 L conical base tanks containing full strength seawater (~34) held at ~26 °C and placed in large polyethylene bags that were then inflated with oxygen-enriched compressed air. Each bag was then stored in a polystyrene box and transported by road for 30 min from the hatchery to Matilda Bay, 15 km upstream from the mouth of the Swan-Canning Estuary. The bags were immersed in the nearshore (<1.5 m deep) waters at this site for 15 min to allow equilibration to ambient water temperature, and then opened and the hatchery-reared PL12s released along a 50 m stretch of the nearshore waters, directly over a bed of the seagrass *Halophila ovalis* (Fig. 1). The first release (March 2015) was carried out at ~19:30 h, at least 30 minutes after sunset, subsequently referred to as ‘night’, while the second release (March 2016) was at ~12:00 h, i.e. during the day. An onshore breeze was present during both releases, which ensured that the PL12s remained within the release area. Salinity, water temperature and dissolved oxygen concentration were measured using a Yellow Springs International Model 556 water quality meter (www.yisi.com) at three different points along the shore. The water at the release site had an average salinity of 34.5 and 33.6, temperature of 25.1 and 27.9 °C and dissolved oxygen concentration of 5.42 and 8.81 mgL<sup>-1</sup> in 2015 and 2016, respectively.

### *Fish faunal sampling*

The fish fauna of a 100 m stretch of the nearshore waters of Matilda Bay was sampled on four occasions in both March 2015 and March 2016 using a 21.5 m seine net. The seine net comprised of two 10 m long wings (6 m of 9 mm mesh and 4 m of 3 mm mesh) and a 1.5 m bunt (3 mm mesh), fished to a maximum depth of 1.5 m and swept an area of 116 m<sup>2</sup>. Fish were sampled during the day and night, twice prior to and twice after the release of the ~130,000 prawns to describe composition and density of the fish fauna in the day and the night, both before and after the release. The first post-release sampling was carried out 2 h after prawns were released to allow enough time for the PL12s to be predated upon by the resident fish fauna, but not enough time for them to become so digested that they could not be accurately identified from the stomach contents (Klumpp and Nichols, 1983; Rosenthal and Paffenhofer, 1972; Fig. 2). This minimised the risk of confusing the PL12s with other potential prey species of similar morphology, such as amphipods (e.g. *Corophium minor* and *Caprella scaura*), mysids (e.g. *Gastrosaccus sorrentoensis*) and caridean shrimp (e.g. *Palaeomonetes australis* and *Palaeomonetes atrinubes*) that also occur in the estuary (Tweedley et al., 2016a; Wildsmith et al., 2011). The second sampling was undertaken eight and 14 h after a day and night release, respectively.

On each sampling occasion, a minimum of 12 replicate seine net samples were collected over ~2 h from a 100 m stretch of nearshore waters that encompassed the area where the prawns were released. Every individual of every fish species collected in six of the  $\geq 12$  samples was retained, euthanized in an ice slurry and subsequently frozen. The total number of individuals of each fish species in these six 'complete' samples was recorded and the total length of each individual measured to the nearest 1 mm, except when a large number of any one species was caught, in which case the lengths of a random subsample of 50 individuals were measured. For the less abundant species, additional individuals from the remaining  $\geq 6$  samples were used to supplement the numbers of stomachs examined. Where possible, a total of 30 individuals across a wide size range were collected for each fish species recorded on each of the eight sampling occasions.



### *Multivariate analyses of fish faunal composition*

Fish assemblage composition was compared statistically between Year (2015, 2016), Diel phase (day, night) and Release (before, after) using a three-factor Permutational Analysis of Variance (PERMANOVA; Anderson et al., 2008). All factors were considered fixed and crossed, and the null hypothesis of no significant difference among *a priori* groups rejected if  $P < 0.05$ . Prior to analysis, the variability in the numbers of individual species in the replicate samples was used to carry out dispersion weighting for each species, which down-weights the effects of those species whose numbers exhibited large differences among replicate samples due to schooling (Clarke et al., 2006). This was achieved by dividing the counts for each species by its mean index of dispersion (i.e. average of the variance to mean ratio in replicate samples) and ensures that all species have similar variability structures, and prevents the analyses becoming dominated by large outliers. These data were then square-root transformed to down-weight the contributions of species with consistently high values (across replicates within a group) in relation to those with consistently low values (Clarke et al., 2014a).

These pre-treated data were then used to construct a Bray-Curtis resemblance matrix and analysed using the three-way PERMANOVA described above. Due to the low number of degrees of freedom in each of the factors, Monte Carlo testing, using the asymptotic permutation distribution was used to provide a more robust indicator of the level of significance. Trends in the data were visualised using a centroid non-metric Multidimensional Scaling Ordination plot (Clarke et al., 2014a). The plot was constructed from a distance among centroids matrix, which averages the samples representing a particular *a priori* group (in this case Year  $\times$  Diel phase  $\times$  Release) in full-dimensional space from the Bray-Curtis resemblance matrix.

When a significant difference between the faunal compositions of *a priori* group(s) was detected, Similarity Percentages (SIMPER; Clarke et al., 2014a) were used to identify those

species that typified the ichthyofaunal composition of each group and those that were responsible for distinguishing between the fish compositions in each pair of groups. A shade plot, derived from the dispersion-weighted and square-root transformed data averaged for each Year and Diel phase combination, was constructed and used to visualise the trends exhibited by the abundance of all teleost species recorded. This shade plot is a simple visualisation of the frequency matrix, where a white space for a species demonstrates that particular teleost was not collected, while the depth of shading from grey to black is linearly proportional to the abundance of the species (Clarke et al., 2014b; Valesini et al., 2014). Species are clustered based on their Bray-Curtis similarities and placed in optimum serial order, constrained by the cluster dendrogram (Clarke et al., 2014a).

#### *Determination of dietary composition*

The total length (TL) of each fish caught and retained for dietary analyses on each of the eight sampling occasions was measured to the nearest mm and weighed to the nearest 0.1 g. The fullness of each stomach was recorded on a scale of 0 (empty) to 10 (fully distended; Platell and Potter, 2001). All dietary items in each stomach were identified to the lowest possible taxonomic level using a dissecting microscope and taxonomic descriptions. The contribution of each dietary item to the total volume of the dietary components (%V) was then estimated visually (Hynes, 1950; Hyslop, 1980). The number of postlarval *M. dalli* in each stomach was counted (Fig. 2).

Dietary components were identified and allocated to one of 19 different minor dietary categories, which were grouped into seven major dietary categories following Platell and Potter (2001). When a dietary item had undergone extensive digestion and could not be identified, it was classified as unidentifiable material (UID). This material, which constituted generally <10 % of the overall dietary volume of each species, was excluded from further analyses. Sand was also not included in the analyses as it was presumably ingested during the

capture of other prey items. The percentage frequency of occurrence (%F) for each minor dietary category within each of the species of fish was calculated.

Stacked bar graphs were constructed to display the mean volumetric contributions of each major dietary category to illustrate whether dietary composition differed (i) among species and within a species with (ii) increasing body size and (iii) between day and night. The focus of this was to identify which of the numerous fish species present at the time of the releases of the ~130,000 hatchery-reared postlarval *M. dalli* feed on postlarvae and, if so, at what body size and during what time of day.

#### *Estimating predation on released prawns*

Relative estimates of the number of hatchery-reared *M. dalli* postlarvae consumed by each of the predator species, on each of the four sampling occasions after the releases (i.e. day and night following both a day and night release), were made by bootstrapping using 1,000 replicates (Fig. 3). The densities of each predator species found in the fish community samples (individuals 100 m<sup>-2</sup>), excluding the proportion of fish from that species with an empty stomach (see Table 4), were multiplied by the average number of *M. dalli* consumed by individuals of that species. This latter value was determined by subtracting an estimate of the ‘natural’ predation from that found in the individual specimen. The estimate of ‘natural’ predation is the average number of *M. dalli* found in the stomachs of that species collected before the release of hatchery-reared prawns and thus is an approximation of the number of wild-spawned postlarval *M. dalli* consumed. *Acanthopagrus butcheri* longer than 150 mm TL were excluded from the abundances, as individuals of this size did not consume released postlarval *M. dalli* (see Results).

The bootstrapping process was used to generate 1,000 estimates for the number of *M. dalli* consumed by each predator species 100 m<sup>-2</sup> during the night and day following the night release, and day and night following the day release (i.e. four sampling occasions in total). The consumption rates for each selected species were then combined to produce a total

predation rate immediately after the release and some hours later, enabling a quantitative assessment of the number of restocked *M. dalli* consumed following separate day and night releases of the same number of prawns. As the sampling efficiency of the seine net for each species is unknown, the estimated numbers of prawns consumed are relative.

## Results

### *Fish faunal composition*

A total of 15,576 teleosts from 24 species were recorded in the 48 seine nets when the entire sample was retained and quantified (Table 1). The total number of species recorded at night (21) was greater than in the day (16) and total fish density was over five times greater at night than during the day (i.e. 475 vs 84 individuals 100 m<sup>-2</sup>). Thirteen species (55 %) were caught in both diel periods, together representing >99 % of the total number of fish, however, the densities and percentage contributions of these species differed markedly (Table 1). For example, the densities of the small bodied atherinids *Atherinosoma elongata* and *Leptatherina presbyteroides* were ~60 and 120 times greater, respectively, at night. This trend was also exhibited by some of the larger-bodied species, such as the apogonid *O. rueppellii* and sparid *A. butcheri*, albeit to a lesser extent. In contrast, densities of the tetraodontid *Torquigener pleurogramma* and the tetrapontids *Pelates octolineatus* and *Amniataba caudavittata* were approximately twice as great during the day than night (Table 1).

Three-way PERMANOVA demonstrated that the composition of the fish fauna differed significantly between Year, Diel phase and the Year × Diel phase interaction, but not Release (Table 2). The percentage mean square for Diel phase (34 %) was higher than any other term in the PERMANOVA, followed by Year (27 %) and then their interaction (17 %). The centroid nMDS plot shows the points representing samples collected during the day were located on the left side of the plot, clearly separated from those collected at night (Fig. 4). Day samples from 2015 were clearly separated, while corresponding night samples were

overlain on each other, explaining the Year  $\times$  Diel phase interaction (Table 2). Points representing the samples collected before and after the release in each Diel phase  $\times$  Year combination were located in close proximity, explaining the lack of a significant difference for any term in the model with Release as a factor (Table 2; Fig. 4).

SIMPER analyses demonstrated that the day samples in both years were typified by *T. pleurogramma*, whilst *O. rueppellii*, *L. presbyteroides* and *A. vaigiensis* characterized the fauna at night. This same suite of species distinguished between these two times of day, with the first species being more abundant during daylight hours, and the latter three prevalent at night (Appendix 1). Although the abundances of some species, such as the highly schooling atherinids *A. vaigiensis*, *Craterocephalus mugiloides*, *A. elongata* and *L. presbyteroides*, differed among years, clear diel differences were still present, with these species being far more abundant during the night than day (Fig. 5).

#### *Overall dietary composition*

The stomach contents of 1,208 individual fish, representing 16 of the most abundant teleost species collected before and after the releases of  $\sim$ 130,000 hatchery-reared postlarval *M. dalli* were examined, with particular focus placed on elucidating the dietary composition of the 929 fish collected after the releases (Table 3). Individuals of the gobiid *Arenigobius bifrenatus*, clupeid *Nematalosa vlaminghi* and sparid *Rhabdosargus sarba* were excluded from further analysis due to the low number of stomachs processed, combined with their minor contribution to the total fish community (Table 1). Fish from a wide size range were examined, ranging from 17 mm total length (*Favonigobius punctatus*) to 282 mm (*A. butcheri*; Table 3). With the exception of the gobiids and atherinids, the stomachs of  $>75$  % of individuals of other species contained food (Table 3).

Among the seven major dietary categories, crustaceans were found in 75 % of the teleost species (12), followed by molluscs (10), annelids and sipunculids (9) and macrophytes and teleosts (both 7). Crustaceans comprised by far the largest mean volumetric contribution

(42 %), with macrophytes (9 %) and molluscs (8 %) being the next most important contributors as the remaining four categories all represented <5 % (Table 3).

Eight of the 13 teleost species consumed postlarval *M. dalli*, with the volumetric contribution ranging from 0.7 % in *A. butcheri* to >25 % for *L. presbyteroides* (26 %), *C. mugiloides* (40 %) and *A. vaigiensis* (47 %; Table 3). This prey species was most frequently recorded in the stomachs of *O. rueppellii*, *L. presbyteroides* and *A. vaigiensis* (12, 46 and 71 %F, respectively). Other small crustaceans, such as isopods and amphipods, comprised substantial components of the dietary composition of *O. rueppellii* (75.2 %), *A. caudavittata* (60.6 %) and *P. olorum* (48 %; Table 3). Macrophytes were consumed in relatively large quantities (i.e. >20 %V) by four species, particularly *P. octolineatus* representing 50 %V of all stomach contents (Fig. 6). Gastropods and bivalves made a substantial contribution to the diets of *A. butcheri*, and *T. pleurogramma*, while annelids and sipunculids were consumed mainly by the gobiids *F. punctatus* and *P. olorum*. Teleosts were predated on by seven of the species, but made a notable contribution to the volume of the overall stomach contents of only *A. elongata*, with this small-bodied atherinid also feeding on teleost eggs. Although poorly represented in the guts of most species, terrestrial arthropods (i.e. arachnids and hexapods) represented 41 %V of the stomach contents of *T. pleurogramma* (Table 3; Fig. 6).

#### *Size related changes in diet*

Postlarval *M. dalli* were consumed by all size classes of *O. rueppellii* (20-79 mm TL) and *A. vaigiensis* (40-99 mm TL; Fig. 7a, b). *Metapenaeus dalli* represented between 4 and 23 %V of the stomach contents of *O. rueppellii* and, combined with other crustaceans, contributed 97 %V of the diet in all, except the largest size class (>60 mm TL = 63 %V), which also fed on teleosts (26 %V). Other crustaceans and *M. dalli* represented the vast majority of the diet of each size class of *A. vaigiensis* (i.e. 88 to 100 %V), but with no particular trend with increasing body size (Fig. 7b). These two dietary groups, and predominantly other crustaceans, also made significant contributions (>50 %V) to each size

class of the gobiid *F. punctatus* (Fig. 7c). Postlarval *M. dalli* were recorded only in the 20-39 mm TL *F. punctatus* size class, while benthic prey, such as annelids and molluscs, were present in substantial volumes in the larger size classes (40 %V in the 20-39 mm class, and 48.1 %V in the 40-59 mm class; Fig. 7c). No size-related shift in dietary composition was detected in the two size classes of *A. elongata* (Fig. 7d).

Among the larger-bodied species, only *A. butcheri* consumed postlarval *M. dalli*, albeit in relatively small amounts. The volume of this prey item decreased from 3 %V for 50-99 mm TL fish to 1 %V in 100-149 mm TL fish and was not found in any of the larger individuals (Fig. 7e). This matched a general decrease in the volume of crustaceans and teleosts consumed with increasing size and corresponding increase in molluscs, which represented 91 %V in the largest size class (Fig. 7e). The volumetric contributions of crustaceans to the diets of *T. pleurogramma* decreased markedly with ontogeny, from 98 %V in the smallest size class to 9 and 0 %V in the largest classes, while those of macrophytes, terrestrial arthropods, molluscs and teleosts increased (Fig. 7f). Contributions of crustaceans to the diet of *A. caudavittata*, and particularly *P. octolineatus*, also declined with increasing body size (Fig. 7g, h).

#### *Diel changes in diet*

The volumetric contributions of hatchery-reared *M. dalli* consumed during the day and night were similar for *O. rueppellii* (9 and 13 %V), *A. vaigiensis* (59 and 56 %V), *F. punctatus* (10 and 14 %V) and *A. butcheri* (1 and 1 %V; Fig. 8). In contrast, greater volumes of *M. dalli* were recorded at night for *L. presbyteroides* and *C. mugiloides*. The overall dietary composition for *A. elongata* and *T. pleurogramma* and, to a lesser extent *A. caudavittata* and *A. butcheri*, differed markedly between diel periods. However, *M. dalli* was either absent or represented a minimal proportion of the diet (~1 %V) in all of these species. *Atherinosoma elongata* fed on crustaceans (100 %V) during the day, but the proportion of this major prey category declined markedly at night (20 %V) and being replaced by teleost eggs (63 %V; Fig. 8g). Diel changes in the diet of *T. pleurogramma* were due to substantial volumes of

terrestrial arthropods being consumed only during daylight hours (Fig. 8k). While the diet of *A. caudavittata* comprised predominantly crustaceans during the day (91 %V), the contribution of this dietary category declined at night (51 %V), due to the increased contribution of macrophytes (1 %V day and 36 %V night; Fig. 8h).

#### *Number of M. dalli consumed*

Of the six species found to consume relatively substantial numbers of prawns (*A. vaigiensis*, *L. presbyteroides*, *C. mugiloides*, *O. rueppellii*, *F. punctatus* and *A. butcheri*), only *A. vaigiensis* consumed postlarval *M. dalli* prior to the release of the hatchery-reared prawns, albeit in very small amounts (average of 0.45 *M. dalli* per fish, with a maximum of 6). Of the fish collected after the releases, the highest mean number of *M. dalli* recorded in the stomachs of any single species, across any of the sampling occasions, was 28 (maximum number = 300; Fig. 2) for *O. rueppellii* collected immediately following the night release. The majority of predation on *M. dalli* by *O. rueppellii* was ascribed to 40-59 mm TL individuals, with all predation occurring after the night release. The atherinid *A. vaigiensis* consumed an average of 18 *M. dalli*, with a maximum of 87, also immediately after the night release. Almost all predation by *A. vaigiensis* was due to individuals in the 40-59 (30 %) and 60-79 mm (69 %) TL size classes. All *M. dalli* consumed by the smaller-bodied atherinids *C. mugiloides* and *L. presbyteroides* were by fish in the 40-59 mm TL size class. All predation by *C. mugiloides* occurred immediately after the night release (average = 23 *M. dalli*), whereas the majority of predation by *L. presbyteroides* occurred following a day release (average = 4.2 and 3.4 *M. dalli* immediately after the day release and the following night, respectively). Very small numbers of *M. dalli* were also consumed by 20-30 mm TL *F. punctatus* during the day following the night release (0.25) and by the 50-99 and 100-149 mm TL size classes of *A. butcheri*, immediately after the day release (0.06 and 0.17, respectively).



### *Estimating predation rates on M. dalli*

The total number of postlarval *M. dalli* consumed by teleost predators was estimated to be 288 % greater following the night than day release, i.e. 2,447 vs 849 *M. dalli* 100 m<sup>-2</sup> (Table 4; Fig. 9). Predation was greater 2 h after a release than during the next diel phase, regardless of whether the release occurred during the night or day. Following the night release, *O. rueppellii* consumed by far the greatest estimated proportion of *M. dalli* (91 %; 2,080 *M. dalli* 100 m<sup>-2</sup>), followed by *A. vaigiensis* (9 %; 207 *M. dalli* 100 m<sup>-2</sup>; Table 4). By the next day, the total predation had decreased greatly; with the estimated total number of *M. dalli* consumed by all species declined to 149 individuals 100 m<sup>-2</sup>, and *O. rueppellii* still the dominant predator (93 %). Following a day release, *A. vaigiensis* was found to be the main predator, responsible for >99 % of the estimated total number of prawns consumed (594 *M. dalli* 100 m<sup>-2</sup>). This proportion decreased to 85 % during the night (216 *M. dalli* 100 m<sup>-2</sup>), with the remaining 15 % consumed by *L. presbyteroides* (Table 4). Thus, although *O. rueppellii* consumed the greatest number of *M. dalli* overall, no *M. dalli* were found in stomachs from the individuals collected following a day release. In contrast, *M. dalli* was found in the stomachs of *A. vaigiensis* regardless of the time-of-release, but in lower numbers than for *O. rueppellii*.

### **Discussion**

This study developed and tested a novel method of estimating predation rates of newly released hatchery-reared postlarval Western School Prawns *Metapenaeus dalli* to identify the optimal time-of-day for their release into the Swan-Canning Estuary. The approach to estimating predation was to determine the relative density of the fish fauna before and after releases, examine the gut contents of likely predators and estimate the total relative number of postlarvae consumed follow a night and a daytime release. Although there was no replication of the night and day releases of prawns, the estimated relative predation rates of postlarval *M. dalli* were much greater when released during the night than the day. This was due mainly to large amounts of predation by *Ostorhincus rueppellii* immediately after the

night release. As such, releasing the postlarval *M. dalli* during the day would improve success of the restocking.

### *Fish faunal composition*

Diel phase significantly influenced the composition of the fish fauna at the release site, with the total number of species and total density of fish at the release site being greater during the night than the day. This increase in both number of species and total density of fish at night is consistent with that recorded in the upper reaches of this system and other estuaries (Gray et al., 1998; Griffiths, 2001; Hoeksema and Potter, 2006; Young et al., 1997) and has been related to predator-prey interactions and feeding-related movements (Yeoh et al., 2017). Atherinids dominated the teleost fauna in the nearshore waters of the release site, as they typically do in south-western Australian estuaries, and microtidal systems throughout the world (Hoeksema et al., 2009; Loneragan et al., 1989; Tweedley et al., 2016b). The densities of three species of atherinids increased markedly at night, which is thought to occur in response to the threat of predation by piscivorous birds, e.g. the cormorant *Phalacrocorax sulcirostris* (Hoeksema and Potter, 2006; Trayler et al., 1989). The apogonid *O. rueppellii* also made a significant contribution to the teleost fauna, and its densities also increased at night. These findings are consistent with those of Kapoor and Khanna (2004), who described members of this family as being nocturnal, and Chrystal et al. (1985) who recorded lower abundances of this species in the deep waters of the Swan-Canning Estuary at night, concluding that they immigrated to shallower waters at this time. Given the substantial diel changes in diet for *O. rueppellii*, their movement into shallow waters at night may also be food-related, due to the emergence of nocturnal crustaceans such as amphipods (Chrystal et al., 1985; Linke et al., 2001).

### *Dietary composition*

The overall dietary composition of the 16 fish species in Matilda Bay varied greatly, indicating that, these teleosts partition dietary resources to reduce competition (Gill and Potter, 1993; Humphries and Potter, 1993; Prince et al., 1982). Crustaceans, however, were identified as a major contributor to dietary composition, occurring in the stomachs of 13 of the 16 species, which may be due to high calorific value of crustaceans (Thayer et al., 1973) and the increased abundance of small crustaceans in seagrass beds (Stoner, 1983). Fishes of a smaller size typically consumed greater proportions of crustaceans, with larger individuals targeting more substantial prey items such as bivalves and teleosts. These larger prey items are more energetically cost effective despite the lower calorific values per gram.

Eight teleost species were found to have ingested postlarval *M. dalli* (i.e. *Atherinomorus vaigiensis*, *Leptatherina presbyteroides*, *Craterocephalus mugiloides*, *O. rueppellii*, *Acanthopagrus butcheri*, *Favonigobius punctatus*, *Pseudogobius olorum*, and *Gerres subfasciatus*), with this prey item making a substantial contribution to the diets of the first six species. Moreover, *M. dalli* represented the greatest proportion of the stomach contents of the first three species, all of which are atherinids. Individuals in this family constitute over 90 % of the total number of fish in the nearshore waters of south-western Australian estuaries (Hoeksema et al., 2009; Tweedley et al., 2016b). Although their high densities are thought to be achieved via resource partitioning (Prince et al., 1982), the fact that *M. dalli* formed a substantial part of the diet of each of *L. presbyteroides*, *A. vaigiensis*, and *C. mugiloides* after the releases indicates that these species are opportunistic and will all feed on an abundant prey item if the opportunity arises.

Crustaceans, including *M. dalli*, dominated the diet of *O. rueppellii* during both diel periods, indicating that although their abundance increased markedly at night, they remained a threat to hatchery-reared prawns regardless of the time of day. The diet of this species differed with ontogeny, with copepods being mainly consumed by small individuals, and teleosts predominantly by larger fish, likely due to increasing mouth size enabling the ingestion of larger prey (Chrystal et al., 1985; Linke et al., 2001). Despite this trend, all size classes of

*O. rueppellii* (20-80 mm TL) consumed hatchery-reared postlarval *M. dalli*. This indicates that prawns released at the PL12 stage prawns (~4 mm TL; Jenkins et al., 2017) are vulnerable to predation by all sizes of *O. rueppellii* present. Thus, these prawns are small enough to be consumed by 20–39 mm fish, whilst still occurring in large enough densities and of a high enough calorific value (Thayer et al., 1973) to be targeted by the large 60–79 mm fish.

The stomach contents of *A. butcheri* were particularly diverse, comprising items from 19 different minor dietary categories, paralleling previous findings for this species (Chuwen et al., 2007). Postlarval *M. dalli* contributed <1 %V to the diet of *A. butcheri*, which is similar to the small volumes (1.1 %V) found by Sarre et al. (2000) in the diet of this species in the same estuary twenty years earlier. More recently, Buckland et al. (2017) also found penaeids in the gut content of only one of the 30 *A. butcheri* they studied.

#### *Predation on postlarval Metapenaeus dalli*

Of the six species that consumed considerable quantities of postlarval *M. dalli*, only *A. vaigiensis* consumed postlarvae before either of the release events, albeit in very small amounts. These wild-spawned postlarvae were of a similar size to the hatchery-reared individuals (Broadley et al., 2017). The difference in consumption of postlarval prawns before and after release indicates that these six teleost species will feed on postlarval *M. dalli* opportunistically, and that the abundance of these prawns in the sampling area was much lower before than after the release of ~130,000 hatchery-reared individuals. Such a view is consistent with the generally broad array of dietary items that these teleosts were found to consume, and that, with the exception of *A. butcheri*, *M. dalli* was not found previously in the diets of these species in the Swan-Canning Estuary (Chrystal et al., 1985; Gill and Potter, 1993; Prince et al., 1982).

After the releases, far greater volumetric contributions of postlarval *M. dalli* were found in the stomachs of the atherinids *L. presbyteroides*, *A. vaigiensis*, and *C. mugiloides* than

*O. rueppellii*, whereas, in terms of number of prawns eaten, the vast majority were consumed by *O. rueppellii*. This indicates that in this case, the percentage volumetric contribution is not a good measure of predation impact on *M. dalli*, as it standardises across predator morphology and size, and the amount of food it consumes. The contribution of *M. dalli* to the diet of *O. rueppellii* was similar during the day and night (9 and 13 %V, respectively), as was the average gut fullness (2.4 and 2.8 out of 10, respectively), yet nearly four times the numbers of *M. dalli* were consumed at night than in the day (12.5 vs 3.4 postlarvae per fish). Thus, *O. rueppellii* likely feeds during both the night and day, but released postlarval *M. dalli* may be more susceptible to predation at night (see below).

From the relative abundance of the predator species, and the number of *M. dalli* they consumed, an estimated ~99 % of the post-release predation on *M. dalli* was attributed to two species: *O. rueppellii* (67.6 %) and *A. vaigiensis* (30.9 %). The estimated number of *M. dalli* consumed by *O. rueppellii* after the night release was 14 times greater immediately after the release at night than the following day. *Metapenaeus dalli*, like many other penaeids, are active during the night and remain buried in the substratum during the day (Park and Loneragan, 1999; Wassenberg and Hill, 1994). Following release at night, postlarval *M. dalli* typically remain within the water column, rather than hiding on the benthos (B. Poh, Murdoch University, personal observation), which makes them more vulnerable to predators. This predation risk is compounded by the nocturnal behaviour of *O. rueppellii*, which immigrate into the shallow, nearshore waters during the night (Chrystal et al., 1985). Predation in the day following the night release was reduced, as the remaining *M. dalli* may have acclimated to the conditions at the release site and buried in the substratum, and individuals of *O. rueppellii* would have emigrated back to deeper waters. These mechanisms would also explain the much lower predation by *O. rueppellii* on postlarval *M. dalli*, following the daytime release.

The small numbers of *M. dalli* present in the diets of *A. vaigiensis* before each release of hatchery-reared postlarvae, compared to the much larger numbers after releases, indicates that the diet of this teleost is influenced by the abundance of prey, as is the case in nearby

coastal waters, despite the difference in invertebrate composition between these two environments (Hourston et al., 2004; Tweedley et al., 2015).

The combined predation of postlarval *M. dalli* across all species was greatest immediately after the release and substantially less during the next diel phase, regardless of whether postlarvae were released in the night or day. Predation on released postlarvae is likely reduced with time following release due to the combined effects of: (i) prawns being dispersed away from the exact point of release by currents/swimming, and also losses to predation, both of which will reduce their abundance and make them less susceptible to opportunistic predators; and (ii) prawns recovering from the stress of the release, adjusting to their environment and thus become less vulnerable. Furthermore, as research suggests that hatchery-reared individuals are generally more susceptible to predation than wild conspecifics (e.g. Brown and Laland, 2001; Stunz and Minello, 2001; Young et al., 2008), exposing *M. dalli* to predators in the hatchery might increase their predator avoidance abilities, as has been shown in other species (e.g. Brown and Smith, 1998; Fu, 2015; Mirza and Chivers, 2000).

In the current study, only teleosts below 150 mm total length consumed postlarval *M. dalli*, with most predation undertaken by individuals in the 40-59 mm size class. Such a trend is likely due to the small size of the postlarvae (~4 mm TL; Jenkins et al., 2017) and the fact that the diet of fish species changes with increasing body size (Coulson et al., 2015; Lek et al., 2011). If larger *M. dalli* are produced for release, as has been done for release programs of *Penaeus chinensis* in China (Wang et al., 2006) and *Penaeus japonicus* in Japan (Hamasaki and Kitada, 2006), i.e. ~30 mm TL, 1 g wet weight, they are likely to be vulnerable to a different range of predators. However, the stocking of juvenile rather than postlarval *P. orientalis* and *P. japonicus* resulted in an increase in the fishery yield, which Bell et al. (2005) attributed to better predator avoidance. Furthermore, modelling studies on releases of *Penaeus esculentus* in northern Australia also suggest that the optimal size-at-release is ~10 mm carapace length (~40 mm TL and 1 g; Loneragan et al., 2004; Ye et al., 2005). Moreover, releases of postlarval *Penaeus* (= *Melicertus*) *plebejus* released at 13 mm

TL into an estuary in New South Wales, Australia, made a significant contribution to recreational prawn catches in this intermittently closed system (Taylor, 2017). Investigating the effect of size-at-release of *M. dalli* is therefore an important consideration for future research.

### *Conclusion and future directions*

This study detected marked diel changes in the abundance and diet of teleost predators, and the number of hatchery-reared postlarval *M. dalli* consumed, indicating that releasing hatchery-reared postlarval *M. dalli* into vegetated nearshore waters during the day is likely to result in much less predation than at night. Although daytime releases potentially expose postlarvae to increased predation from *A. vaigiensis*, they would greatly reduce the predation risk posed by *O. rueppellii*, which consumed by far the greatest numbers of *M. dalli*. The diel variation in abundance and diet of individual fish species at the release site makes it difficult to select a release time when predation by all fish species is reduced. The methodological approach developed here helps to resolve this dilemma as it combines (i) the effect of predator abundance and (ii) the magnitude of predation on the target prey species, allowing quantitative comparisons to be made across species and times-of-release. Thus, a sound judgement, based on empirical evidence, can be made in determining the best time to release hatchery-reared *M. dalli*.

The method devised in the current study could readily be applied to determine whether alternative sites-of-release would provide a more suitable environment with lower predation pressure. While the abundance and survival of some penaeids, such as *P. esculentus*, is related to the presence of aquatic macrophytes (Loneragan et al., 2013), this relationship has not been established for *M. dalli*. Moreover, the abundance of *O. rueppellii* and *A. vaigiensis*, which were responsible for 68 and 31 % of the total predation at the release site, fluctuated in the nearby Peel-Harvey Estuary commensurate with changes in the extent and biomass of macrophytes (Potter et al., 2016). Therefore, releasing hatchery-reared postlarval *M. dalli* over unvegetated substrates may facilitate greater survival, due to reduced abundances of its

key teleost predators over bare substratum during the day. However, as the abundance, feeding behaviour and diet of fish differ in different habitats (Linke et al., 2001; Schafer et al., 2002), and unvegetated areas offer less shelter, further investigation will be required to determine the suitability of the bare sandy areas as potential release sites.

### **Acknowledgements**

This project was supported through funding from the Fisheries Research and Development Corporation (FRDC 2013/221) on behalf of the Australian Government, the Department of Parks and Wildlife (RSPMUR01), Murdoch University and the Recreational Fishing Initiatives Fund. All work was conducted in accordance with Murdoch University Animal Ethics Permit #RW2664\_14. Gratitude is expressed to Kyle Hodson for helping to process some of the samples, and to our friends and colleagues who assisted with the fieldwork.

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## Figure captions

**Fig. 1.** Maps showing (a) the location of the Swan-Canning Estuary in temperate southwestern Australia and (b) the location of Matilda Bay in the Swan-Canning Estuary where the hatchery-reared postlarval *Metapenaeus dalli* were released and where the fish fauna were sampled, and photographs of (c) a postlarval *M. dalli* ~4 mm total length at release size. Photograph (c) provided by the Australian Centre for Applied Aquaculture Research.

**Fig. 2.** Photograph of the stomach contents of (a) a 45 mm total length (TL) *Ostorhinchus rueppellii* showing large numbers of postlarval *Metapenaeus dalli* ( $n = 300$ ) and (b) a 52 mm TL *Craterocephalus mugiloides*, with much smaller numbers ( $n = 2$ ).

**Fig. 3.** Flow chart detailing the methodological approach used to derive the relative estimated number of *Metapenaeus dalli* consumed by teleost predators and confidence limits for consumption, following releases during the day and night.

**Fig. 4.** Non-metric multidimensional scaling ordination plots constructed from a distance among centroids matrices output from a Bray-Curtis resemblance matrix, derived from the dispersion weighted and square-root transformed abundances of each fish species recorded in Matilda Bay in the Swan-Canning Estuary for each Year  $\times$  Diel phase  $\times$  Release combination. Day (●); Night (●); Before release (B); After release (A).

**Fig. 5.** Shade plot of the dispersion weighted and square-root transformed densities (per 100 m<sup>-2</sup>) of each fish species recorded in Matilda Bay in the Swan-Canning Estuary for each Diel phase  $\times$  Year combination. White areas denote the absence and grey scale the abundance of a species. Day (●); Night (●).

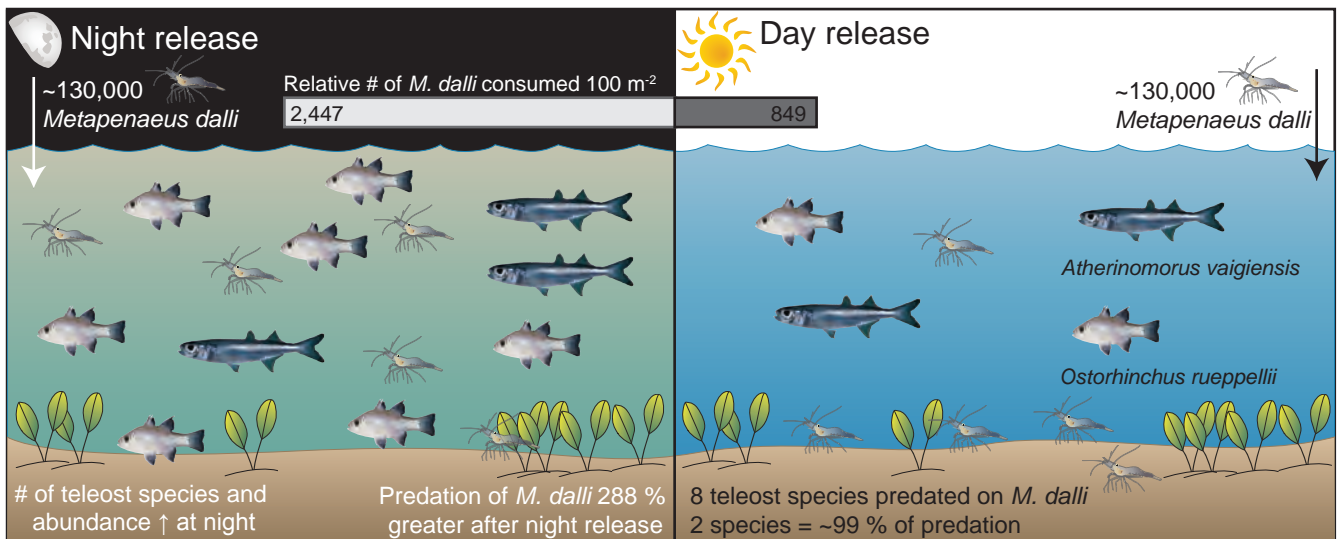
**Fig. 6.** The mean percentage volumetric contributions (%V) of various major dietary categories and *Metapenaeus dalli* to the diets of 13 teleost species recorded in Matilda Bay in the Swan-Canning Estuary, temperate south-western Australia. The numbers of stomachs examined for each species are given in parentheses. *L. pre*, *Leptatherina presbyteroides*; *A. vai*, *Atherinomorus vaigiensis*; *C. mug*, *Craterocephalus mugiloides*; *O. rue*, *Ostorhinchus rueppellii*; *F. pun*, *Favonigobius punctatus*; *P. olo*, *Pseudogobius olorum*; *G. sub*, *Gerres subfasciatus*; *A. but*, *Acanthopagrus butcheri*; *A. cau*, *Amniataba caudavittata*; *A. elo*, *Atherinosoma elongata*; *P. oct*, *Pelates octolineatus*; *S. bur*, *Sillago burrus*; *T. ple*, *Torquigener pleurogramma*.

**Fig. 7.** The mean percentage volumetric contributions (%V) of various major dietary categories and *Metapenaeus dalli* to the diets of sequential total length (LT) classes of eight abundant teleost species collected after the release of hatchery-reared postlarval *M. dalli* into Matilda Bay. Note that plots for *Craterocephalus mugiloides* and *Leptatherina presbyteroides* are not presented as they were represented by a single size-class (see Fig. 7). The numbers of stomachs examined are given in parentheses. Full species names are given in Table 1.

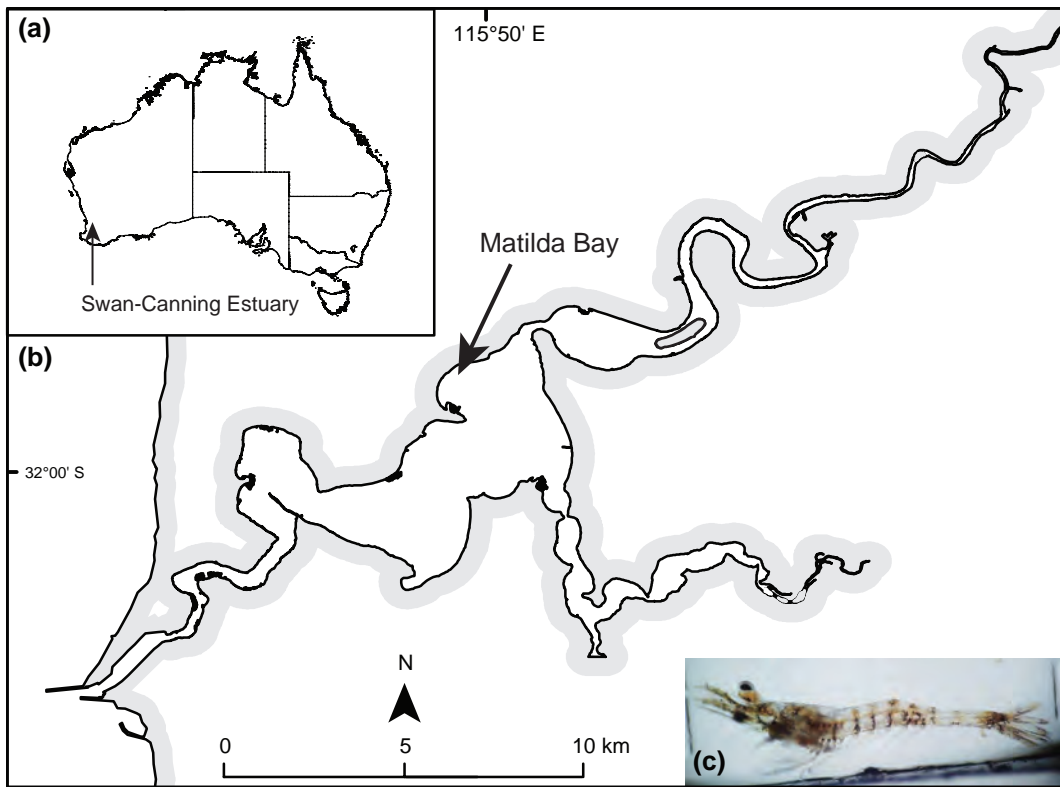
**Fig. 8.** The mean percentage volumetric contributions (%V) of various major dietary categories and *Metapenaeus dalli* to the diets of ten teleost species collected during the day and night after the release of hatchery-reared postlarval *M. dalli* into Matilda Bay. The numbers of stomachs examined are given in parentheses. Full species names are given in Table 1.



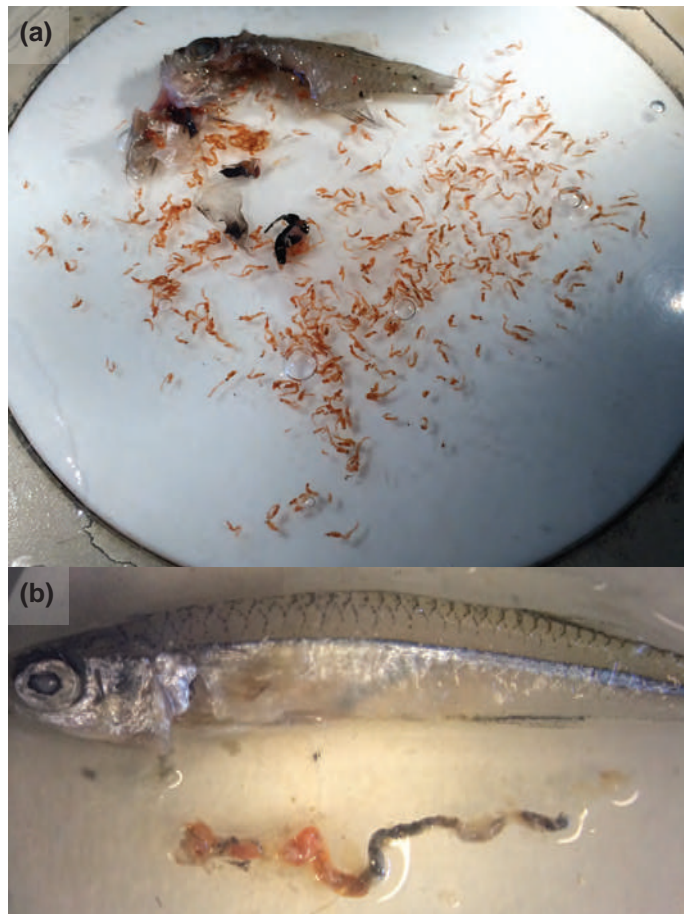
**Fig. 9.** The relative estimated number of postlarval *Metapenaeus dalli* consumed 100 m<sup>-2</sup> of Matilda Bay during the night and day, before and after the release of ~130,000 hatchery-reared *M. dalli*. Full species names are given in Table 1.



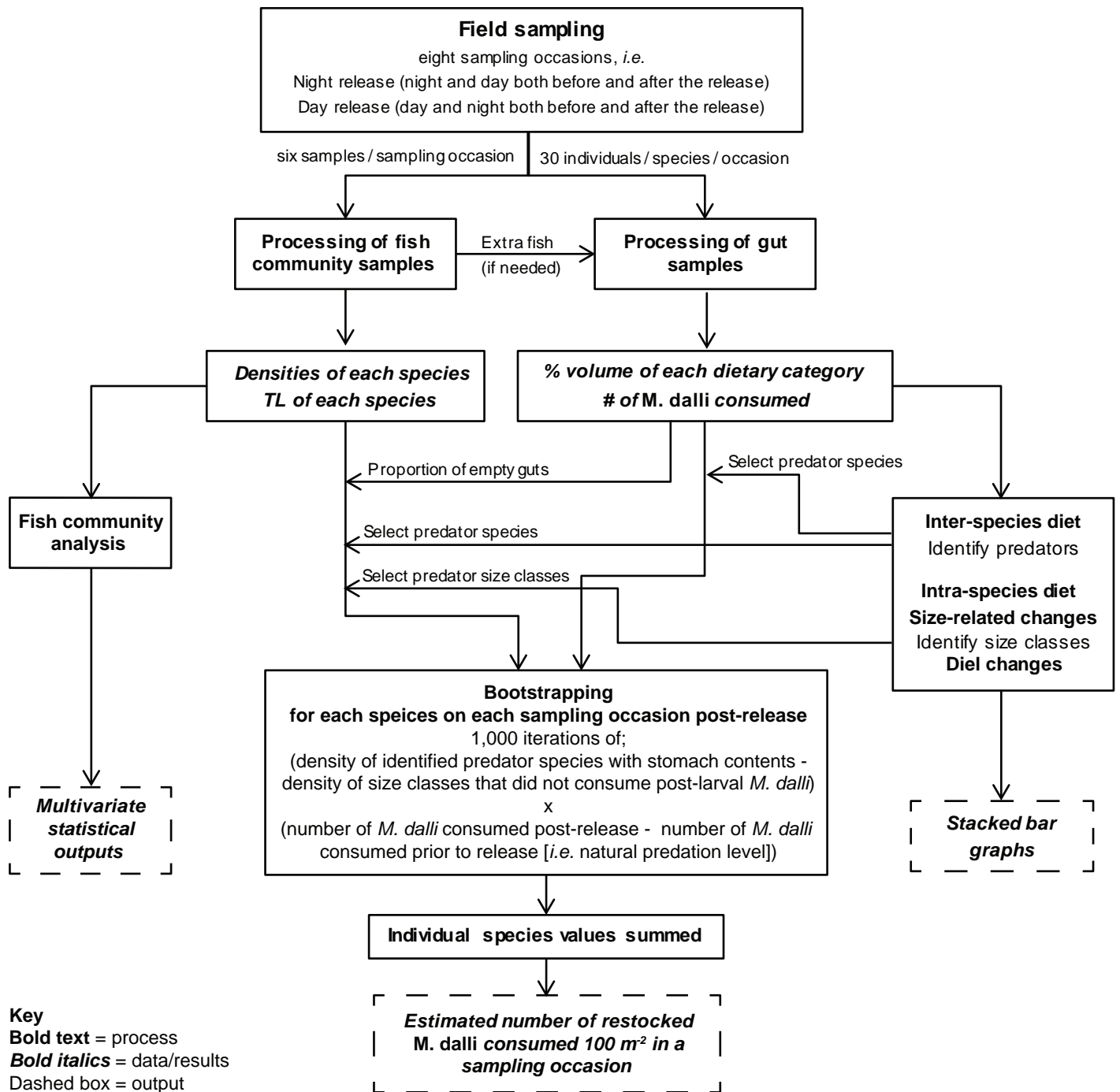
**Graphical abstract**



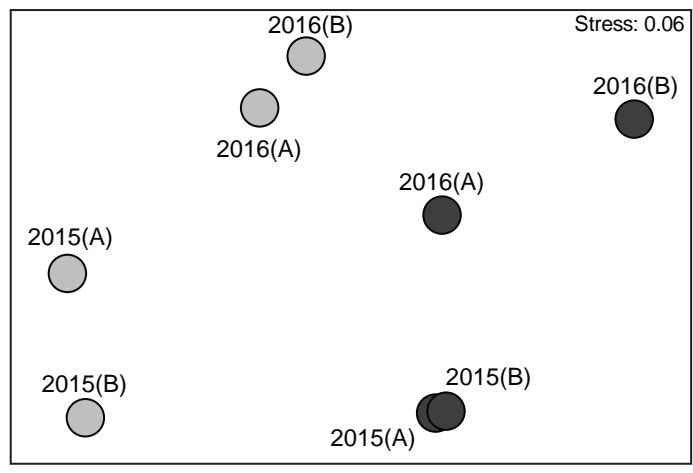
**Fig. 1.**



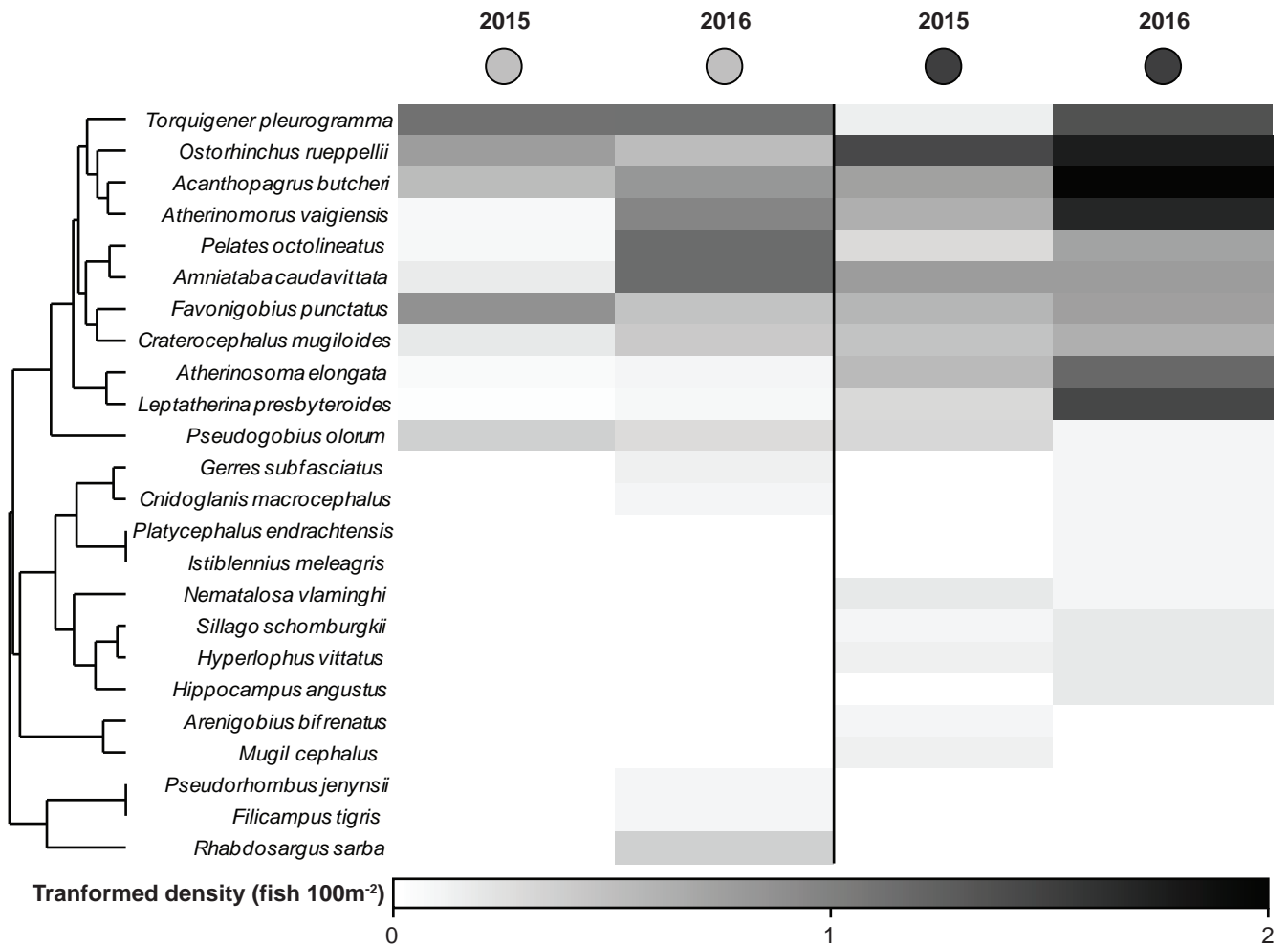
**Fig. 2.**



**Fig. 3.**



**Fig. 4.**



**Fig. 5.**

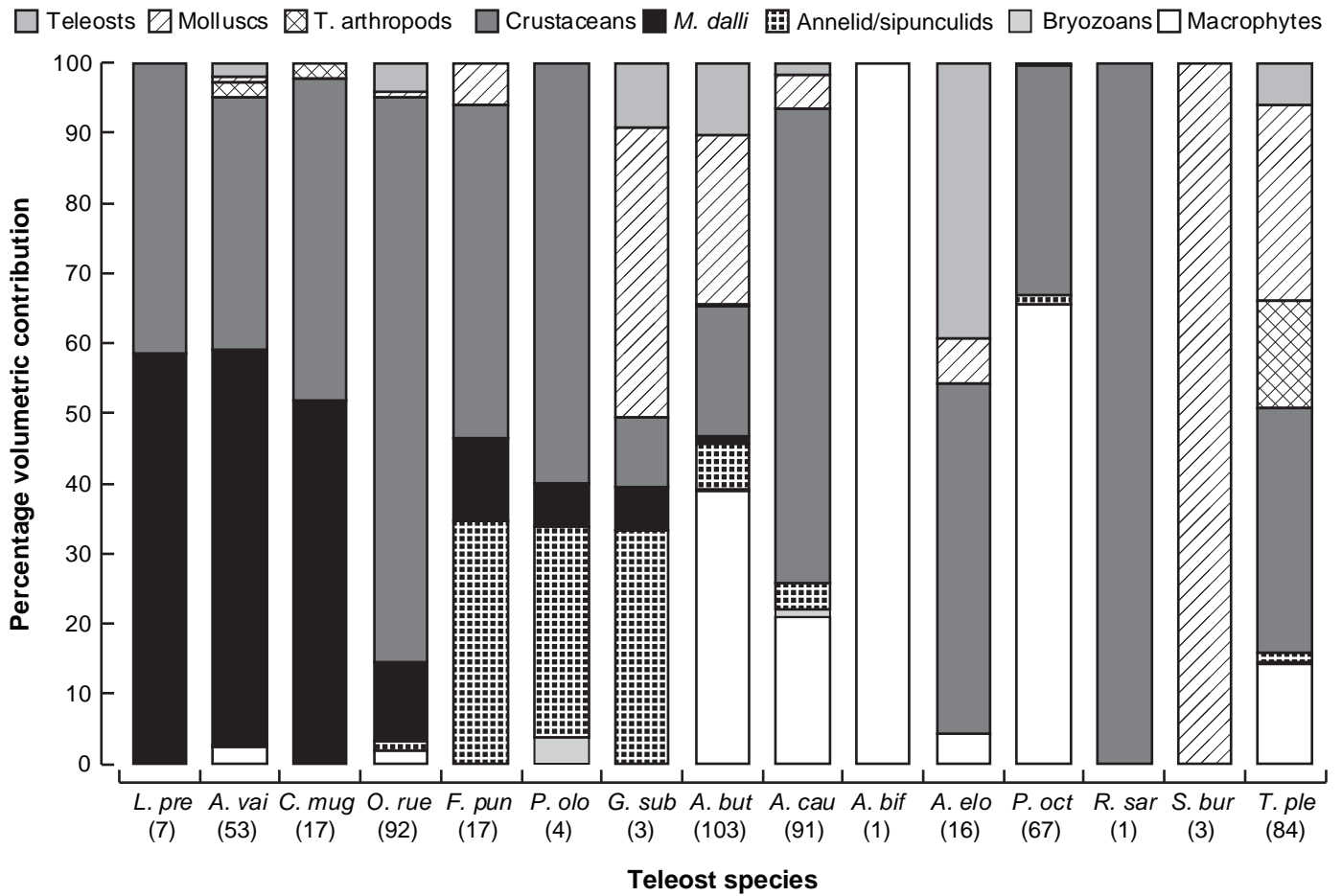
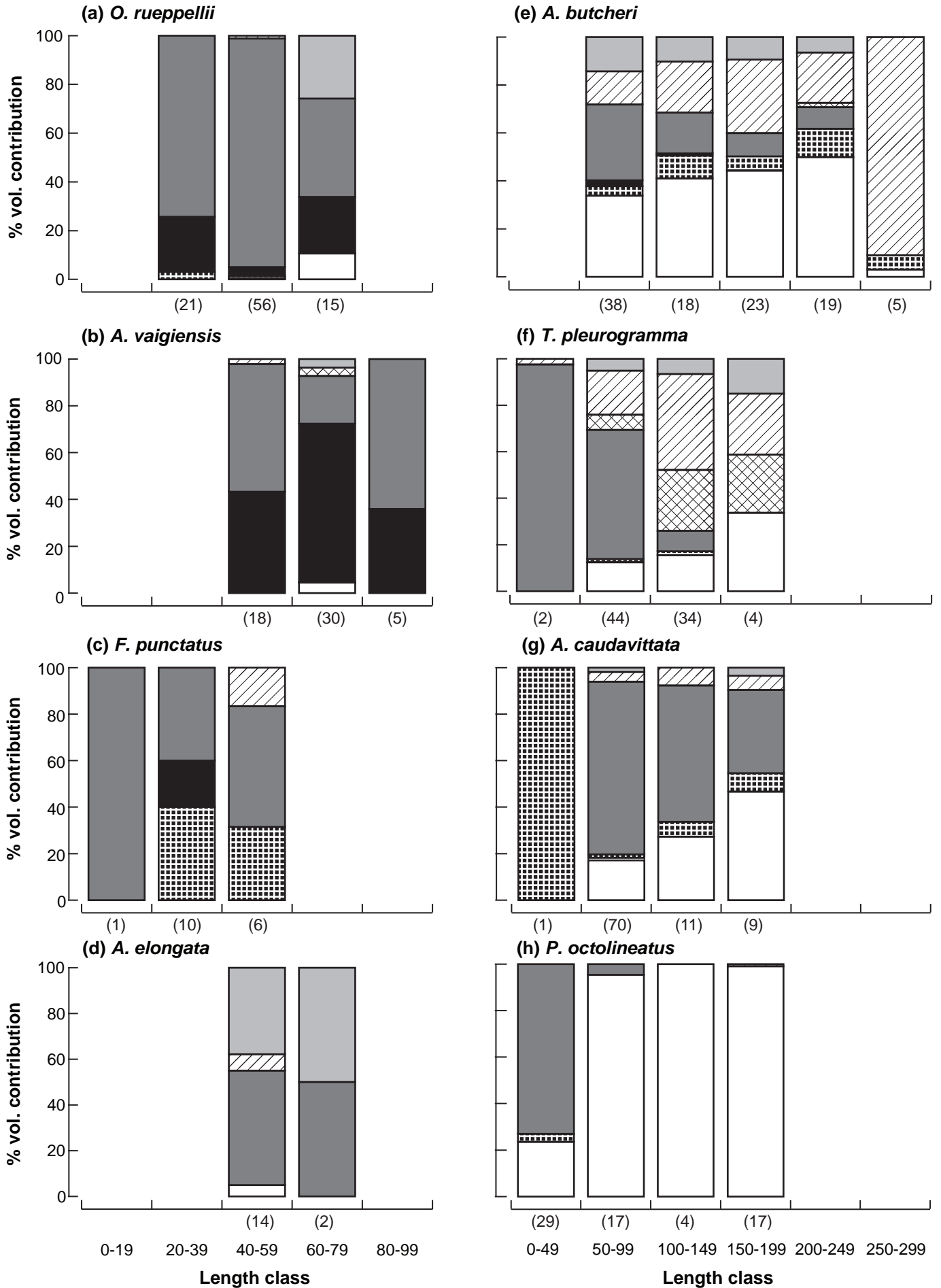


Fig. 6.



Teleosts
  Molluscs
  T. arthropods
  Crustaceans
  *M. dalli*
 Annelid/sipunculids
  Bryozoans
  Macrophytes



**Fig. 7.**

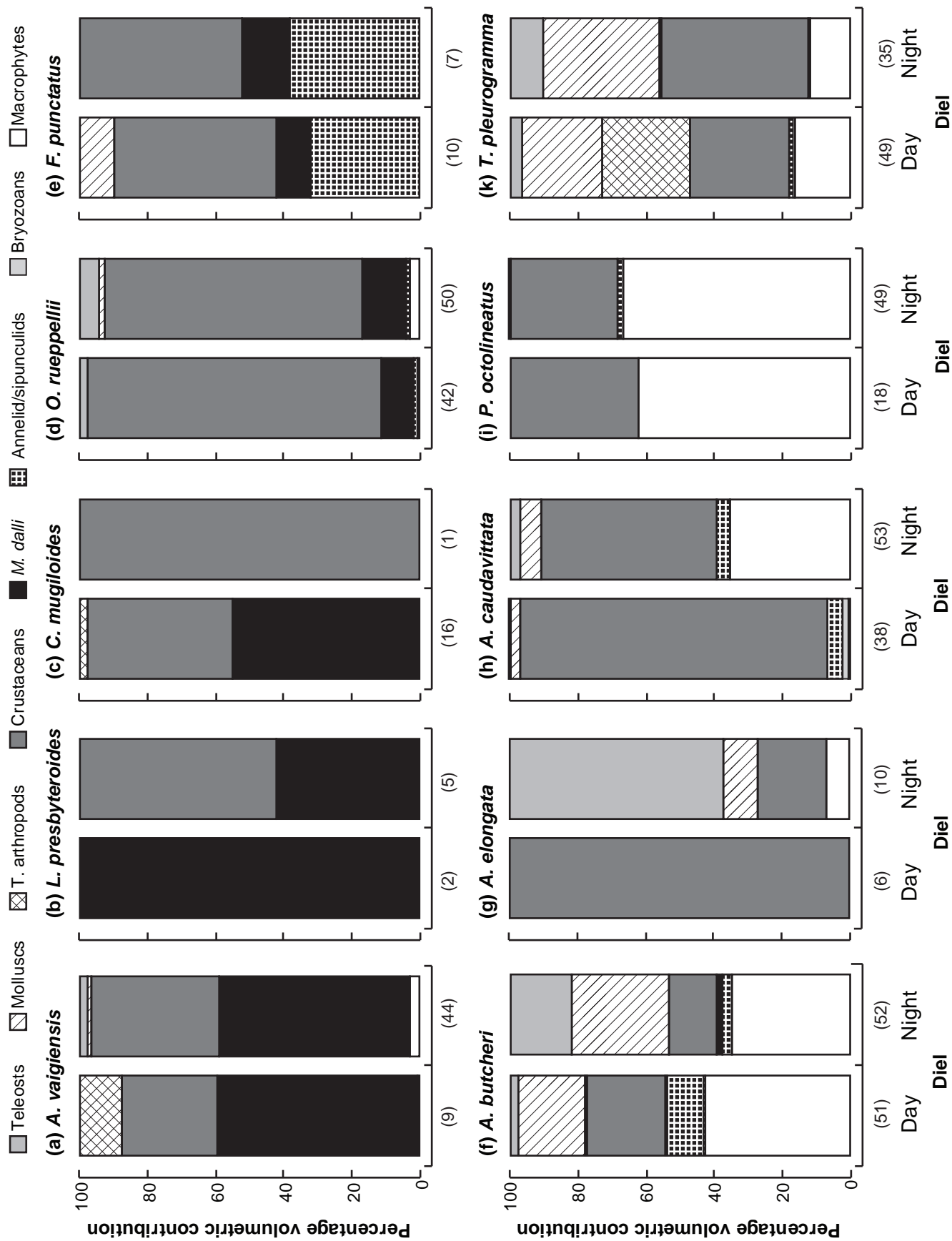


Fig. 8.

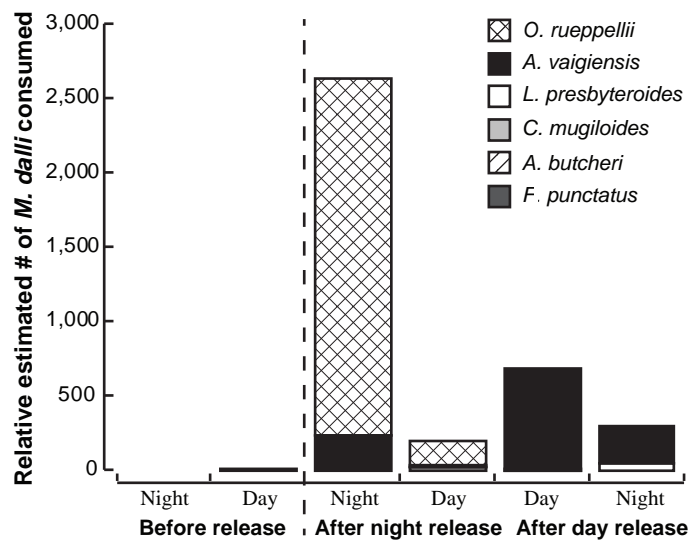


Fig. 9.

**Table 1.** Mean densities (D; numbers of fish 100 m<sup>-2</sup>), standard error (SE), percentage contributions to the total catch (%) and rank by numbers (R) of the fish species caught in seine nets during the day and night at Matilda Bay in the Swan-Canning Estuary during March 2015 and March 2016. Total numbers of species and Total mean density (number of fish 100 m<sup>-2</sup>) are also shown. Grey shading shows species that contributed > 5% to the total abundance.

Species	Total				Day				Night			
	D	SE	%	R	D	SE	%	R	D	SE	%	R
<i>Leptatherina presbyteroides</i>	114.15	57.98	40.81	1	1.80	1.22	2.13	8	226.51	112.43	47.67	1
<i>Atherinosoma elongata</i>	53.43	25.52	19.10	2	1.65	0.69	1.96	9	105.21	49.28	22.14	2
<i>Ostorhinchus rueppellii</i>	49.14	6.71	17.57	3	21.30	5.89	25.26	1	76.98	9.06	16.20	3
<i>Atherinomorus vaigiensis</i>	24.95	5.12	8.92	4	15.73	6.99	18.65	3	34.16	7.13	7.19	4
<i>Pelates octolineatus</i>	14.19	4.49	5.07	5	20.15	8.56	23.89	2	8.23	2.46	1.73	6
<i>Amniataba caudavittata</i>	9.32	2.49	3.33	6	11.39	4.87	13.50	4	7.26	1.07	1.53	7
<i>Acanthopagrus butcheri</i>	5.39	1.03	1.93	7	2.30	0.55	2.73	6	8.48	1.80	1.78	5
<i>Torquigener pleurogramma</i>	4.85	0.88	1.73	8	5.78	1.20	6.86	5	3.92	1.28	0.82	8
<i>Craterocephalus mugiloides</i>	2.26	0.76	0.81	9	2.26	1.42	2.68	7	2.26	0.59	0.48	9
<i>Favonigobius punctatus</i>	1.35	0.24	0.48	10	1.40	0.38	1.66	10	1.29	0.31	0.27	10
<i>Pseudogobius olorum</i>	0.22	0.06	0.08	11	0.25	0.08	0.30	11	0.18	0.09	0.04	11
<i>Hyperlophus vittatus</i>	0.07	0.04	0.03	12					0.14	0.08	0.03	12
<i>Rhabdosargus sarba</i>	0.07	0.03	0.03	12	0.14	0.07	0.17	12				
<i>Nematalosa vlaminghi</i>	0.05	0.03	0.02	14					0.11	0.06	0.02	13
<i>Sillago schomburgkii</i>	0.05	0.03	0.02	14					0.11	0.06	0.02	13
<i>Gerres subfasciatus</i>	0.05	0.04	0.02	14	0.07	0.07	0.09	13	0.04	0.04	0.01	17
<i>Cnidoglanis macrocephalus</i>	0.04	0.03	0.01	17	0.04	0.04	0.04	14	0.04	0.04	0.01	17
<i>Hippocampus angustus</i>	0.04	0.03	0.01	17					0.07	0.05	0.02	13
<i>Mugil cephalus</i>	0.04	0.04	0.01	17					0.07	0.07	0.02	13
<i>Filicampus tigris</i>	0.02	0.02	0.01	17	0.04	0.04	0.04	14				
<i>Platycephalus endrachtensis</i>	0.02	0.02	0.01	17					0.04	0.04	0.01	17
<i>Istiblennius meleagris</i>	0.02	0.02	0.01	17					0.04	0.04	0.01	17
<i>Arenigobius bifrenatus</i>	0.02	0.02	0.01	17					0.04	0.04	0.01	17
<i>Pseudorhombus jenynsii</i>	0.02	0.02	0.01	17	0.04	0.04	0.04	14				
<b>Number of seine nets</b>		<b>48</b>				<b>24</b>				<b>24</b>		
<b>Number of species</b>		<b>24</b>				<b>16</b>				<b>21</b>		
<b>Total mean density</b>		<b>280</b>				<b>84</b>				<b>475</b>		

**Table 2.** Mean squares (MS), *pseudo-F* ratios (*pF*), and significance levels without Monte Carlo testing (*P*) and with (*P mc*) from a three-way PERMANOVA of the fish communities recorded in Matilda Bay in the Swan-Canning Estuary during March 2015 and March 2016. *df* = degrees of freedom. Significant results are highlighted in bold.

<b>Factor</b>	<b><i>df</i></b>	<b>MS</b>	<b>% MS</b>	<b><i>pF</i></b>	<b><i>P</i></b>	<b><i>P mc</i></b>
<i>Main effect</i>						
Diel phase (Day, Night)	1	<b>12917</b>	<b>34.0%</b>	<b>11.20</b>	<b>0.001</b>	<b>0.001</b>
Year (2015, 2016)	1	<b>10241</b>	<b>27.0%</b>	<b>8.88</b>	<b>0.001</b>	<b>0.001</b>
Release (Before, After)	1	2409	6.3%	2.08	0.057	0.069
<i>Interactions</i>						
Diel phase × Year	1	<b>6523</b>	<b>17.2%</b>	<b>5.65</b>	<b>0.001</b>	<b>0.001</b>
Diel phase × Release	1	2221	5.8%	1.93	0.066	0.078
Year × Release	1	1532	4.0%	1.32	0.237	0.239
Year × Diel phase × Release	1	1000	2.6%	0.87	0.549	0.534
Residual	40	1153	3.0%			

**Table 3.** Mean percentage volumetric contribution (%V) and frequencies of occurrence (%F) of the different dietary items and categories (boldface) found in the stomachs of 16 teleost species recorded in Matilda Bay in the Swan-Canning Estuary from samples collected two hours after the release of hatchery-reared postlarval *Metapenaeus dalli*.

Dietary item	<i>A. but</i>		<i>A. cau</i>		<i>A. bif</i>		<i>A. vai</i>		<i>A. elo</i>		<i>C. mug</i>		<i>F. pun</i>		<i>G. sub</i>	
	%V	%F	%V	%F	%V	%F	%V	%F	%V	%F	%V	%F	%V	%F	%V	%F
Algae	12.1	29.4	20.3	24.5	100.0	100.0	2.3	10.2								
Seagrass	16.9	44.0	0.1	2.1					3.2	4.5						
<b>Macrophytes</b>	29.0	67.0	20.4	26.6	100.0	100.0	2.3	10.2	3.2	4.5						
Bryozoa	0.0	0.9	0.9	2.1												
<b>Bryozoans</b>	0.0	0.9	0.9	2.1												
Platyhelminthes	0.1	0.9	0.1	1.1									2.6	4.3		
Sipunculids	0.2	0.9														
Annelids	6.1	17.4	1.8	10.6			0.1	1.7					17.0	26.1	10.0	25.0
UID ann./sip.	0.0	0.9														
<b>Annelid/sipunculids</b>	6.4	18.3	1.9	11.7			0.1	1.7					19.6	30.4	10.0	25.0
<i>Metapenaeus dalli</i>	0.7	2.8					46.7	71.2			40.0	40.9	7.8	8.7	2.5	25.0
<i>Penaeus latisulcatus</i>	0.4	4.6														
<i>Alpheus</i> spp.																
Brachyurans	2.3	8.3	0.7	4.3												
Mysids	1.4	2.8														
Isopods	5.5	24.8	31.6	59.6					4.5	4.5	5.0	9.1	0.4	4.3		
Amphipods	3.7	11.0	27.2	64.9			0.9	5.1			0.5	4.5	17.8	26.1	7.5	25.0
Copepods	0.7	0.9	1.0	5.3			26.4	37.3	4.5	4.5	3.2	4.5	7.8	13.0		
UID Crustaceans			0.1	1.1			4.7	5.1	25.9	27.3	22.7	22.7				
<b>Crustaceans</b>	14.7	38.5	60.6	73.4			78.7	86.4	35.0	36.4	71.4	77.3	33.9	47.8	10.0	50.0
Arachnids											0.5	4.5				
Hexapods	0.3	1.8					1.9	3.4			1.4	4.5				
<b>Terrestrial arthropods</b>	0.3	1.8					1.9	3.4			1.8	9.1				
Gastropods	4.3	20.2	2.7	10.6												
Bivalves	13.4	28.4	0.5	3.2					0.2	4.5			3.0	4.3	25.0	50.0
UID molluscs	2.7	5.5	1.1	3.2			0.7	1.7								
<b>Molluscs</b>	20.4	45.0	4.3	16.0			0.7	1.7	0.2	4.5			3.0	4.3	25.0	50.0
Teleosts	9.0	22.9	1.7	5.3			1.9	3.4	28.6	31.8					3.8	25.0
<b>Teleosts</b>	9.0	22.9	1.7	5.3			1.9	3.4	28.6	31.8					3.8	25.0
Detritus	1.4	3.7	5.6	9.6			3.2	3.4	8.9	9.1	9.1	9.1	8.3	17.4	12.5	25.0
Sand	10.7	33.9	0.3	5.3			0.2	1.7	5.9	18.2	8.2	13.6	33.0	65.2	38.8	75.0
UID	8.0	14.7	4.5	9.6			11.1	16.9	18.2	18.2	9.5	13.6	2.2	13.0		
Mean stomach fullness	4.2		5.1		6.0		2.1		0.7		1.1		1.1		3.2	
# stomachs	118		100		1		92		78		57		49		5	
# stomachs full	109		94		1		59		22		22		23		4	
% stomachs full	92.4		94.0		100.0		64.1		28.2		38.6		46.9		80.0	
Mean total length	141		87		78		66		51		47		32		157	
Median total length	130		70		78		66		52		47		33		159	
Total length range	64-282		48-195		78-78		40-104		41-67		34-56		17-50		135-175	

Dietary item	<i>L. pre</i>		<i>O. rue</i>		<i>P. oct</i>		<i>P. olo</i>		<i>S. bur</i>		<i>T. ple</i>		<i>N. vla</i>		<i>R. sar</i>	
	%V	%F	%V	%F	%V	%F	%V	%F	%V	%F	%V	%F	%V	%F	%V	%F
Algae			1.9	4.1	46.1	57.0					7.6	29.1				
Seagrass					4.4	6.3					4.8	19.8				
<b>Macrophytes</b>			1.9	4.1	50.5	59.5					12.3	43.0				
Bryozoa							3.0	20.0			0.1	1.2				
<b>Bryozoans</b>							3.0	20.0			0.1	1.2				
Platyhelminthes																
Sipunculids																
Annelids			1.2	3.1			14.0	40.0			1.0	4.7				
UID ann./sip.					1.3	1.3										
<b>Annelid/sipunculids</b>			1.2	3.1	1.3	1.3	14.0	40.0			1.0	4.7				
<i>Metapenaeus dalli</i>	26.4	45.5	10.4	12.2			5.0	20.0								
<i>Penaeus latisulcatus</i>																
<i>Alpheus</i> spp.											1.0	1.2				
Brachyurans											2.8	7.0				
Mysids																
Isopods	9.1	9.1	22.3	39.8	11.1	20.3	26.0	40.0			20.2	45.3			60.0	100.0
Amphipods			49.7	64.3	9.0	17.7	22.0	40.0			6.3	17.4			40.0	100.0
Copepods	17.3	27.3	3.2	10.2	5.9	15.2					0.5	5.8				
UID Crustaceans																
<b>Crustaceans</b>	52.7	63.6	85.6	90.8	26.0	30.4	53.0	60.0			30.9	52.3			100.0	100.0
Arachnids																
Hexapods											14.8	24.4				
<b>Terrestrial arthropods</b>											14.8	24.4				
Gastropods											13.8	36.0				
Bivalves									22.0	60.0	12.4	24.4				
UID molluscs			0.7	1.0	0.1	1.3										
<b>Molluscs</b>			0.7	1.0	0.1	1.3			22.0	60.0	26.3	52.3				
Teleosts			3.9	6.1							5.2	9.3				
<b>Teleosts</b>			3.9	6.1							5.2	9.3				
Detritus	18.2	18.2	3.6	4.1	20.6	26.6	20.0	20.0			1.6	3.5	50.0	50.0		
Sand	4.5	9.1	3.1	9.2	0.9	2.5			78.0	100.0	6.4	22.1	50.0	50.0		
UID	24.5	27.3			0.6	2.5	10.0	20.0			1.5	5.8				
Mean stomach fullness	0.2		2.5		6.0		1.3		3.4		3.2		4.5		1.0	
# stomachs	97		129		81		7		5		107		2		1	
# stomachs full	11		98		79		5		5		86		2		1	
% stomachs full	11.3		76.0		97.5		71.4		100.0		80.4		100.0		100.0	
Mean total length	51		47		74		34		152		106		179		110	
Median total length	52		45		47		34		156		99		179		110	
Total length range	46-58		23-75		22-190		24-43		139-160		35-165		100-258		110-110	

*A. but*, *Acanthopagrus butcheri*; *A. cau*, *Amniataba caudavittata*; *A. bif*, *Arenigobius bifrenatus*; *A. vai*, *Atherinomorus vaigiensis*; *A. elo*, *Atherinosoma elongata*; *C. mug*, *Craterocephalus mugiloides*; *F. pun*, *Favonigobius punctatus*; *G. sub*, *Gerrus subfasciatus*; *L. pre*, *Leptatherina presbyteroides*; *O. rue*, *Ostorhinchus rueppellii*; *P. oct*, *Pelates ootolineatus*; *P. olo*, *Pseudogobius olorum*; *S. bur*, *Sillago burrus*; *T. ple*, *Torquigener pleurogramma*; *N. vla*, *Nematalosa vlaminghi*; *R. sar*, *Rhabdosargus sarba*.

**Table 4.** Estimated number (X) and 95% confidence limits ( $\pm$ CL) of *Metapenaeus dalli* consumed 100 m<sup>-2</sup> of Matilda Bay in the Swan-Canning Estuary by each of the six predator species in the night and day (a) before release (*i.e.* natural levels of predation), and after a (b) night and (c) day release of ~ 130,000 hatchery-reared postlarvae. % represents the percentage contribution each species made to the total number of *M. dalli* consumed on each sampling occasion. Full species names are given in Table 1.

Species	(a) Before Release						(b) After Night Release						(c) After Day Release					
	Night			Day			Night			Day			Day			Night		
	X	$\pm$ CL	%	X	$\pm$ CL	%	X	$\pm$ CL	%	X	$\pm$ CL	%	X	$\pm$ CL	%	X	$\pm$ CL	%
<i>O. rueppellii</i>							2,079.92	57.03	90.94	148.93	6.81	93.32						
<i>A. vaigiensis</i>				2.37	0.15	100.00	207.19	5.87	9.06				594.45	18.23	99.94	215.87	4.56	84.91
<i>L. presbyteroides</i>										0.02	0.00	0.01	0.09	0.008	0.02	38.36	2.53	15.09
<i>C. mugiloides</i>										10.55	0.47	6.61						
<i>A. butcheri</i>													0.25	0.012	0.04			
<i>F. punctatus</i>										0.08	0.01	0.05						
<b>Total</b>	<b>0.00</b>			<b>2.37</b>			<b>2,287.11</b>			<b>159.58</b>			<b>594.79</b>			<b>254.23</b>		
<b>Grand total</b>				<b>2.37</b>						<b>2,446.69</b>						<b>849.02</b>		

**Appendix 1.** Species identified by SIMPER analysis that typified (shaded) and distinguished (non-shaded) the fish faunas of Matilda Bay during the day and night in both (a) March 2015 and (b) March 2016. The text in superscript denotes the diel phase in which each distinguishing species was most abundant.

(a) 2015	Day	Night
Day	<i>Ostorhinchus rueppellii</i> <i>Torquigener pleurogramma</i> <i>Favonigobius punctatus</i>	
		<i>Ostorhinchus rueppellii</i> <i>Amniataba caudavittata</i> <i>Atherinosoma elongata</i> <i>Atherinomorus vaigiensis</i> <i>Leptatherina presbyteroides</i>

(b) 2016	Day	Night
	<i>Torquigener pleurogramma</i> <i>Pelates octolineatus</i> <i>Amniataba caudavittata</i> <i>Acanthopagrus butcheri</i>	
		<i>Acanthopagrus butcheri</i> <i>Ostorhinchus rueppellii</i> <i>Atherinomorus vaigiensis</i> <i>Leptatherina presbyteroides</i>