

# Scale-dependent variation in composition of fish fauna among sandy tropical estuarine embayments

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**ABSTRACT:** Variability in tropical estuarine sandy bottom fish faunas was investigated along a 200 km section of the northeast coast of tropical Australia at 3 nested spatial scales: among bays, among adjacent estuaries within bays, and among replicates within estuaries. Sampling was confined to a single habitat type, shallow sandy habitats, and a single class of estuaries, those with extensive areas of shallow sand in their lower reaches. This approach was employed to minimise the biases inherent in sampling estuaries containing varying proportions of the disparate habitat types that occur in tropical estuaries. The results showed: (1) the compositions of samples from all 9 estuaries in November 1999 were quite distinct from those in July 1999, July 2000 and July 2001; (2) there were no clear differences among estuaries during November 1999, but strong differences among estuaries every July, which were greater than differences among years; and (3) there was a greater difference at the scale of estuaries than at the larger spatial scale of 'bays', such that the differences among estuaries within bays were consistently greater than differences among bays. This pattern was consistent between seasons and among years in the same season. The clear estuary-to-estuary variability suggests that fauna of adjacent estuaries are likely to be no more similar than the faunas of estuaries hundreds of kilometres apart. This implies that no single estuary can be assumed to be a control site that can be used as a baseline against which to judge change in a different 'impacted' estuary.

**KEY WORDS:** Estuary · Fish · Tropical · Distribution · Scale

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## INTRODUCTION

Tropical estuaries are areas of high biological diversity compared to equivalent temperate ecosystems. They vary greatly in their physical natures, often at relatively small spatial scales. For instance, even within Australia's north-eastern tropics, some areas are characterised by substantial rainfall over most of the year, while areas only 100 km away may display marked seasonality, with heavy rainfall confined to a brief wet season each year. Consequently, estuaries in these areas range from wet-tropic habitats, with reduced salinities over much of the year, to dry-tropic habitats that have only a brief period of depressed salinity and which can progress rapidly to hypersaline conditions during the 'dry' season (Sheaves 1996). Additionally, tropical estuaries provide a diversity of habitats, including mangrove forests, intertidal and subtidal sea-

grass beds, sand and mud banks, deep channels, steep 'snaggy' banks, rocky outcrops and open-water environments. This range of habitats provides a variety of niches for colonisation by a diverse community of organisms. Together this diverse species pool and spatially variable environment would seem to afford the opportunity for the development of considerable spatio-temporal variability in faunal composition.

Understanding the pattern and extent of this variability is both central to understanding the structure and function of tropical estuarine faunas and crucial for the success of impact assessment and management. No understanding of the forces that structure tropical estuarine faunas is possible until we develop a full appreciation of the patterns of faunal distribution and the scales at which variability operates. This is because major biological and physical processes are focussed at characteristic spatial scales (Stommel 1963, Schneider

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1994a, Mohd Norowi et al. 1999) and produce characteristic patterns of faunal distribution (Azovsky 2000). Consequently, comparison of variability at different scales can be used to assess both the relative importance of processes operating within an ecosystem (Kratz et al. 1987, Weins 1989) and the scales at which important processes operate. Additionally, successful management requires a full understanding of how estuarine assemblage structure, and the forces creating that structure, vary from place to place. Such knowledge is central to determining if management can be applied at a regional level or whether estuaries must be managed on a case-by-case basis. Further, the tenets of impact assessment require that impacts should be judged relative to changes at a control site (Green 1979). As a consequence, understanding how faunas differ among estuaries is necessary before appropriate control sites and impact assessment strategies can be determined.

Although great estuary-to-estuary variability has been reported in many studies of tropical estuarine fish faunas (e.g. Robertson & Duke 1987, Sheaves 1998), there has been no investigation of scale-specific variability of these faunas. In fact such studies are lacking for most parts of the world. Most studies of tropical estuarine fish assemblages have concentrated on single estuaries (e.g. Blaber 1980, Blaber et al. 1989), rather than comparing faunas between estuaries. Where multiple estuaries have been studied, either only a single scale has been included (e.g. Robertson & Duke 1987, Sheaves 1998) or samples have been collected at unspecified but apparently very different times in different estuaries (Blaber & Milton 1990). The inclusion of only a single scale presents a problem in that there is no way of unambiguously attributing differences between faunas of different estuaries to actual variability at the scale studied.

The picture from past studies of Indo-West Pacific estuaries is of generally similar, identifiably estuarine fish faunas (Robertson & Duke 1987, Blaber & Milton 1990, Sheaves 1998). Despite this overall similarity, authors have invariably reported clear differences between estuaries; however, this observation has to be treated cautiously in light of the deficiencies in these comparisons. For example, Robertson & Duke (1987) studied 4 estuaries separated by 100s of kilometres and found distinct faunas in each. However, the lack of any measure of variability on smaller scales (e.g. between estuaries in each of the 4 regions) meant that there was no way of knowing if these differences were any greater than would be seen if adjacent estuaries had been sampled. Consequently, such comparisons can provide little more than broad indications of the similarities and differences among tropical estuarine fish faunas. Understanding the extent of variability would

help resolve such ambiguities. As well as putting previous studies into context, multiscale studies of variability of tropical estuarine fish assemblages are crucial if future research is to proceed in a more organised and relevant way. Knowing the scale at which substantial variability occurs allows subsequent research to be directed at uncovering the processes underlying that variability. Moreover, understanding where variability is focussed allows spatial replication to be targeted in the most meaningful way.

In this study fish faunas in the lower reaches of 9 estuaries on the north-east coast of tropical Australia were investigated to determine if there was a characteristic scale of variability in fish assemblage composition, the extent of faunal similarity between adjacent estuaries and how consistent these patterns were over time. Variability in taxonomic composition was compared among bays, among estuaries within bays and within individual estuaries, and I investigated whether the pattern of variability was consistent between contrasting seasons and between years.

## MATERIALS AND METHODS

**Site description.** The study was conducted in 3 estuaries, in each of 3 'bays' (see below) on the north-east coast of tropical Australia (Fig. 1). Although different sampling methodologies and the collection of samples at different times make previous studies of tropical Australian fish faunas difficult to compare, the extent of variability reported between faunal compositions suggested that estuary-to-estuary variability was likely to be important. If so, selecting estuaries of very different character (e.g. sand versus mud dominated) would confound differences at the scale of estuaries with differences in the type of estuary sampled. Consequently, to minimise any extraneous variability, the estuaries selected within each bay were close together (in each bay within a span of 20 km or less) and possessed large, sandy lower reaches (2 to 4 km in length). All the estuaries were short, with maximum salt water intrusion of between about 3 and 15 km.

Because this is the first study to consider spatial variability in tropical Australian estuaries on a hierarchy of scales, no information was available on a logical definition of a scale above that of individual estuaries. Capes and headlands are predictable sites of discontinuity of coastal flow patterns (Ebert & Russell 1988), and so are likely to be boundaries to the continuity of physical variables and major biological phenomena such as larval supply. As a consequence, the bays selected appeared to be homogeneous geographical units, delineated by sandy or rocky promontories at either end, or by their location along a large, protected

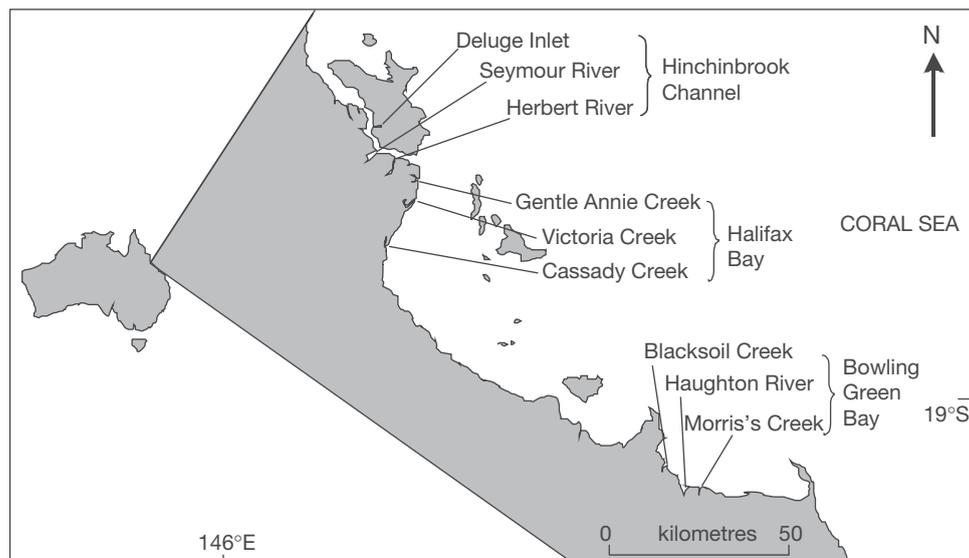


Fig. 1. Location map of the 9 sampling sites along the coast of north-eastern Australia. Latitude and longitude are for the cut away view

coastal waterway (in the case of Hinchinbrook Channel). Thus, bays were selected on the basis of being potentially separate entities in terms of physical environment, climate and larval supply. The closest estuaries of the northernmost bay, Hinchinbrook Channel, and the central bay, Halifax Bay, were only some 15 km apart. However, while Halifax Bay is situated on the open coast and swept by coastal currents with largely unidirectional flows, Hinchinbrook Channel is sheltered by Hinchinbrook Island and is flushed by marine water from both its northern and southern ends (Wolanski et al. 1990). In addition, the structure of Hinchinbrook Channel means that, particularly in the dry season, water is trapped for long periods and exchanged only slowly with coastal waters (Wolanski et al. 1990). Moreover, while the estuaries in Halifax Bay drain coastal lowlands, those in Hinchinbrook Channel drain high-runoff mountainous areas. In contrast, the estuaries in Bowling Green Bay, the southernmost bay, are separated from those in Halifax Bay by some 100 km. Although both Halifax and Bowling Green Bays are swept by unidirectional coastal currents, they are spatially segregated and separated by 2 headlands. Moreover, while Hinchinbrook Channel and Halifax Bay are in the high rainfall 'wet-tropics', Bowling Green Bay is in the much lower rainfall 'dry-tropics'. The separations between the bays was somewhat arbitrary and spatially greater between Hinchinbrook and Halifax and between Halifax and Bowling Green. If this difference was important, it should have been reflected as an interaction between scale and bays in the subsequent analyses.

**Sampling design.** Sampling was conducted in July 1999, November 1999, July 2000 and July 2001. July

is in the cool, dry season, a period of low recruitment (settlement of 0 group fish) for many species, while November is in the hot, early wet season, when recruitment of many species is high. To reduce the influence of among-estuary habitat differences as much as possible, sampling was confined to a single habitat type: shallow (<1 m deep) sandy habitats. Limiting sampling to the sandy lower reaches was necessary because logistic constraints prohibited sampling all habitats in all estuaries. The large variety of gears needed to sample all possible habitats, and the time needed to conduct the sampling would render the comparable sampling of all habitats in 9 estuaries untenable. This obviously limits the interpretation of the results of the study to the habitat type sampled. However, these shallow sandy areas were the dominant habitat in each estuary, comprising at least 90% of the total area, meaning the most common habitat was represented.

Sampling was conducted with 2 identical small pocket seine nets (30 m long, 2 m drop, 11 mm stretched mesh). Nets were set using electric outboard motors by anchoring 1 end of the net to the shore, laying the first 15 m of net out perpendicular to the shore and laying the final 15 m out parallel to the shore, in an upstream direction. A 30 m rope attached to the outer end of the net was taken to the shore as far upstream of the net as possible. This rope was used to haul the open end of the net until it reached the shore, then both ends of the net were hauled simultaneously. In each sampling period during 1999 and 2000 two teams were used to sample each of the 9 estuaries twice over 9 d following the lunar first quarter. This timing provided a period with a series of day-time low tides of similar heights suitable for seine netting. Estuaries

were sampled in random order, with the constraint that consecutive samples at any 1 estuary were collected at least 3 d apart. Six replicate net hauls were taken in each estuary on each sampling day, with the 12 hauls collected from each estuary over each 9 d sampling period taken from independent locations. The locations were spaced haphazardly over the whole potential sampling area of each estuary, with at least 100 m between sampling sites. Because it was clear that sampling each estuary twice did not substantially change the composition of samples, in July 2001 sampling at each estuary was reduced to 9 samples on a single day, to reduce unnecessary field time and minimise the number of fish killed and injured.

Salinity, temperature and turbidity data were collected at each sampling site on each sampling occasion.

**Regression tree analysis.** Patterns of similarity in faunal composition over the 9 estuaries and 4 sampling trips were analysed using multivariate classification and regression trees (mCARTs) (De'ath 2003). Multivariate classification and regression trees are a statistical technique used to explore, describe and predict relationships between multispecies data and explanatory variables. Clusters of samples are formed by repeated splitting of the data, with each split chosen to minimise the dissimilarity (variability) of samples within clusters. At each split, data are partitioned into 2 groups that are mutually exclusive and as homogeneous as possible. Cross-validation is used to estimate the prediction error for the tree of each size that minimises dissimilarity. The 'best'-sized tree is selected on the basis of this estimated prediction error. The 'best' tree is defined as the tree with the lowest cross-validation error (minimum CV-error), or more often the smallest tree within 1 standard deviation of tree with the lowest CV-error (1-SE tree). Each cluster represents a species assemblage. The clusters and their dependence on the explanatory variables are represented graphically by a tree diagram. Multivariate regression trees can be employed on data that are unbalanced, have missing values, non-linear relationships between variables, and/or high-order interactions.

Trees were fitted following the approach of De'ath (2003). Data were first 4th root transformed to reduce the dominance of abundant species. Then, 100 ten-fold cross validations, based on independent random number seeds, were run, and the distributions of: (1) tree sizes with minimum cross-validation error (minimum CV-error) and (2) the smallest trees within 1 standard error of the tree with minimum CV-error (1-SE) were used to select the tree size producing the best fit. A 4-leaf tree was selected under the 1-SE rule 62% of the time, with no other size was selected >30% of the time. Under the minimum CV-error, 3 tree sizes (4, 6 and 7) were selected between 30 and 36% of the time. Although the

1-SE tree is usually considered the most appropriate model, trees between Sizes 4 and 7 were investigated to allow a more in-depth appraisal of the importance of estuary-to-estuary versus bay-to-bay variability.

As a way of summarising these results in pictorial form, non-metric multidimensional scaling (nMDS) (Clarke 1993, Borg & Groenen 1997) was performed on the abundance data, using Bray–Curtis dissimilarities on 4th-root-transformed data. In nMDS, points that are close together show a high level of similarity in species

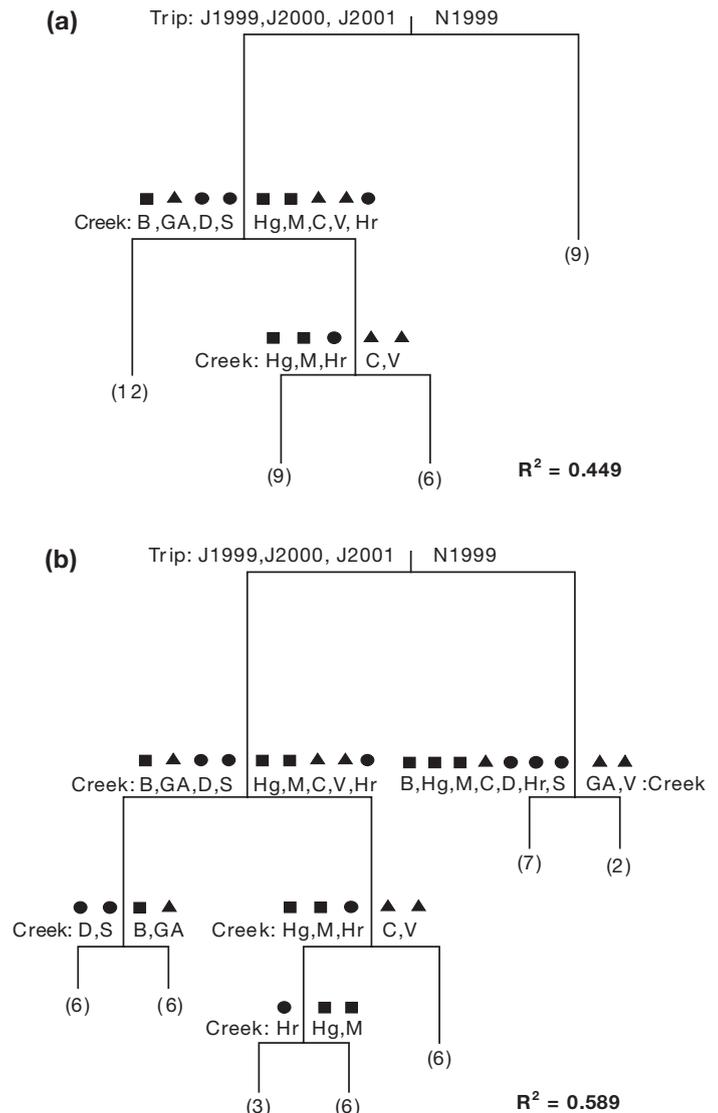


Fig. 2. Multivariate CARTs for spatial and temporal factors using the 22 species occurring in >10% of samples. Abundance data were 4th root transformed. (a) The best tree under the 1 SE error criterion, and (b) the best tree under the minimum CV-error criterion (B: Blacksoil Ck.; C: Cassady Ck.; D: Deluge Inlet; GA: Gentle Annie Ck.; Hg: Haughton R.; Hr: Herbert R.; M: Morris's Ck.; S: Seymour R.; V: Victoria Ck.; ■: Bowling Green Bay; ▲: Halifax Bay; ●: Hinchinbrook Channel). Numbers in parentheses are sample sizes

composition, leading to the interpretation that adjacent points represent more similar faunas than those that are more distant. This is, of course, not an exact representation of the analyses, but a representation of the relationships among data in low-dimensional space that provides more standard visualisation than the less familiar regression trees.

## RESULTS

During the course of the study 117 species of fish were captured, although most catches were dominated by a few numerous species. Catches of all the common species were dominated by juveniles (i.e. the 0 to 1 age group), regardless of the time of year.

### Regression tree analysis

The final mCART model selected under the 1-SE criterion (Fig. 2a), shows 4 major features: (1) the compositions of samples from all 9 estuaries in November 1999 were quite distinct from those in July 1999, July 2000 and July 2001; (2) there were no clear differences between estuaries during November 1999; (3) the July samples formed a group which was not further split by year in the final model, indicating that differences among estuaries were greater than differences among years; and (4) the primary split on the 'July' branch of the tree partitioned at least 1 estuary from each bay to both sides of the split, and only on subsequent splits were the remaining pairs of estuaries grouped together. This suggests that differences among estuaries within bays are consistently greater than differences between bays. Even the best 7-leaf tree (Fig. 2b), the largest tree that would be considered an appropriate fit under the minimum CV-error criterion, included no additional splits due to years, highlighting the consistency of composition within the estuaries among years. The minimum CV-error tree included 3 additional splits, 1 on the November 1999 branch and 2 on the July branch. The split on the November branch separated 2 Halifax Bay sites, Gentle Annie and Victoria Creek, from the rest of the sites. So although 2 sites in 1 bay were similar, there was little difference between all

the rest of the estuaries. In a similar way the additional splits on the July branch tended to group pairs of estuaries together, leaving the third estuary from each bay by itself or grouped with estuaries from a different bay. Overall, although there was some indication of bay-to-bay differences, fish catches in an individual estuary from 1 bay were likely to be as much like those in an estuary from a different bay as those from another estuary in the same bay.

### Ordination

Multidimensional scaling displays these patterns graphically (Fig. 3). November 1999 samples form a group (ellipse in Fig. 3), with little overlap with any of the July samples. Samples from each estuary form fairly discrete groups (polygons in Fig. 3), with no definable year-to-year pattern. There is no consistent similarity within bays. Two estuaries within each bay overlap (e.g. Houghton River and Morris's Creek), but invariably the third estuary in the bay is more similar to those in one of the other bays.

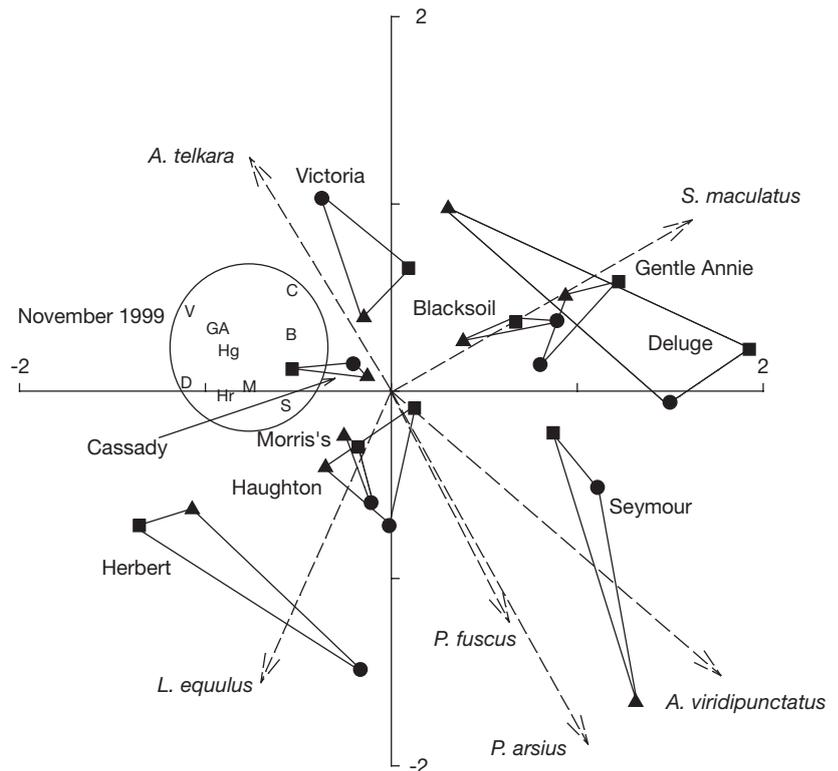


Fig. 3. Two-dimensional solution (stress1 = 0.1665) of non-metric multidimensional scaling of data for all 4 trips. Replicate samples for each estuary have been pooled to give a single value for each estuary. Dashed vectors indicate the direction of greatest increase in abundance of the species most highly correlated with the ordination space. Vector lengths are proportional to  $R^2$  for each species and are scaled up by a factor of 3 (site abbreviations, see Fig. 2; ■: July 1999; ▲: July 2000; ●: July 2001)

**Faunal consistency among estuaries**

Simple profiles of mean abundance of the most common taxa for the 3 sampling trips in July (Figs. 4, 5 & 6) show clear differences in faunal composition among estuaries. However, not only are there clear differences among estuaries, but the profiles of abundance for each estuary were remarkably similar over the 3 samples from July. In the case of all 9 estuaries, the 3 profiles were clearly more similar to each other than

they were to the profiles for any other estuary in any year. This year-to-year consistent pattern of differences existed despite a similarity in composition among estuaries in the November 1999 samples (Fig. 7), which were collected between two of the July samples. The November samples were quite different from July samples, with: (1) much higher abundances of most species, (2) more similarity within bays and (3) profiles that bear little resemblance to the July samples from the same estuary.

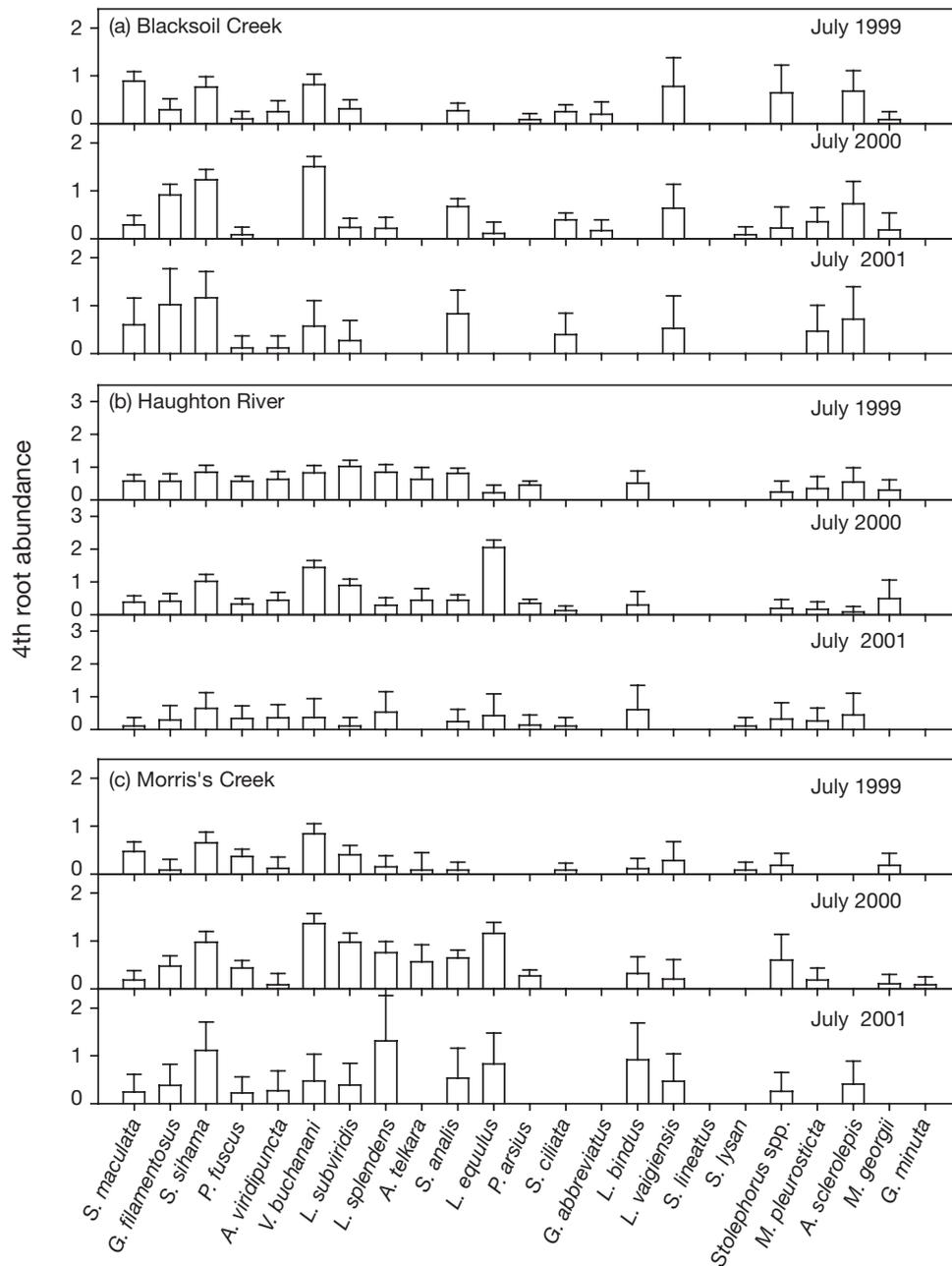


Fig. 4. Mean (4th root transformed) abundances,  $\pm 95\%$  confidence intervals, for species occurring in at least 10% of samples overall: (a) Blacksoil Creek, (b) Haughton River, (c) Morris's Creek

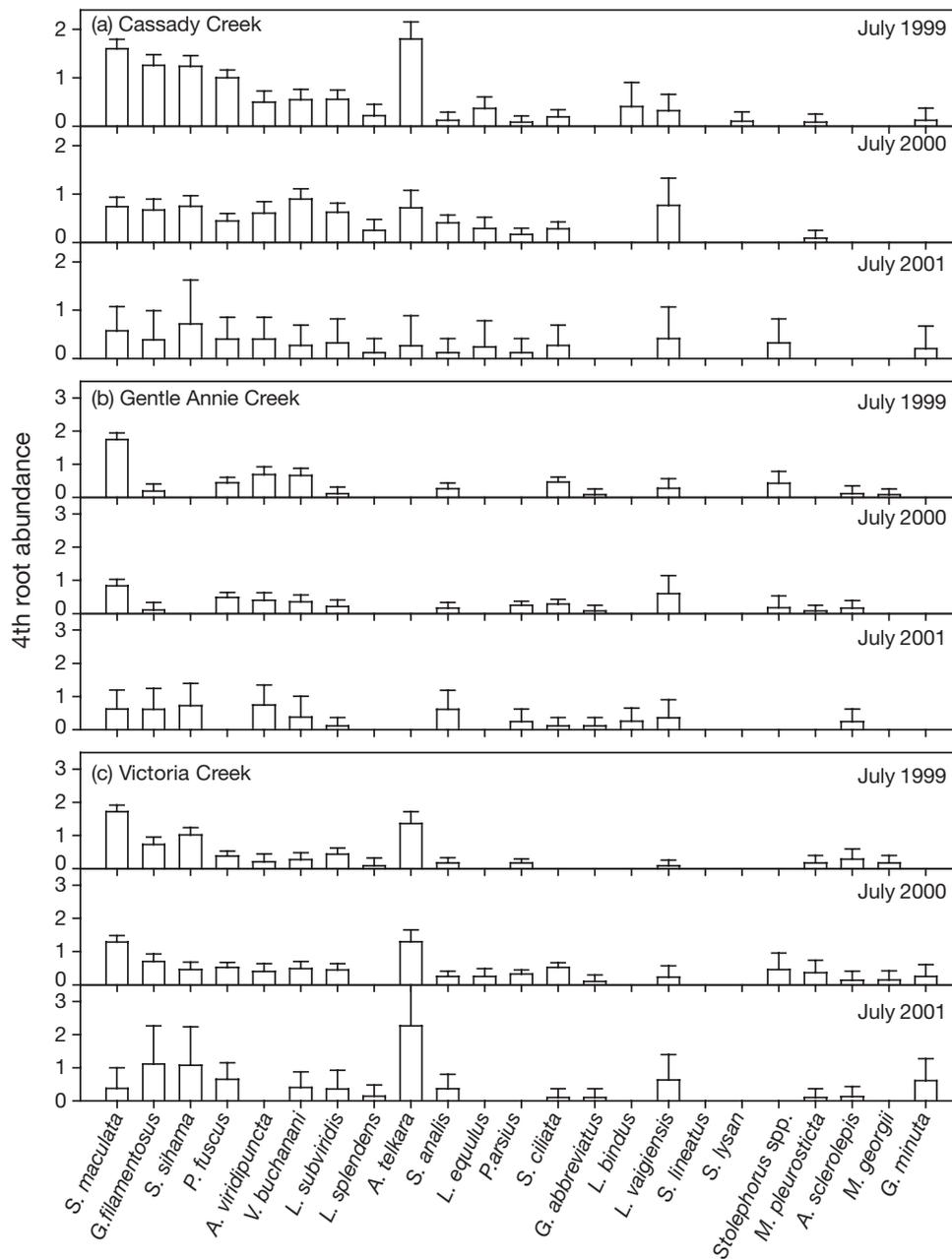


Fig. 5. Mean (4th root transformed) abundances,  $\pm 95\%$  confidence intervals, for species occurring in at least 10% of samples overall: (a) Cassidy Creek, (b) Gentle Annie Creek, (c) Victoria Creek

**Consistency of the physical environment**

Mean salinity levels largely reflected the difference in runoff regime in the 3 bays (Fig. 8). Salinities in the dry-tropical estuaries in Bowling Green Bay were high throughout the study, rarely falling below 30‰. In Halifax Bay salinities were similar to those in Bowling Green Bay in both dry-season samples (July), but were markedly lower in November, particularly in Cassidy and Victoria Creeks. In contrast, salinities in Hinchinbrook Channel estuaries tended to be lower than those

in other bays on most occasions, with the Herbert River having low salinity on all sampling trips. Neither temperature or turbidity (measured as NTU) showed any consistent substantial variability.

**DISCUSSION**

Multivariate analyses of the abundance data highlighted 4 major features. Firstly, the compositions of samples from all 9 estuaries in November 1999 were quite

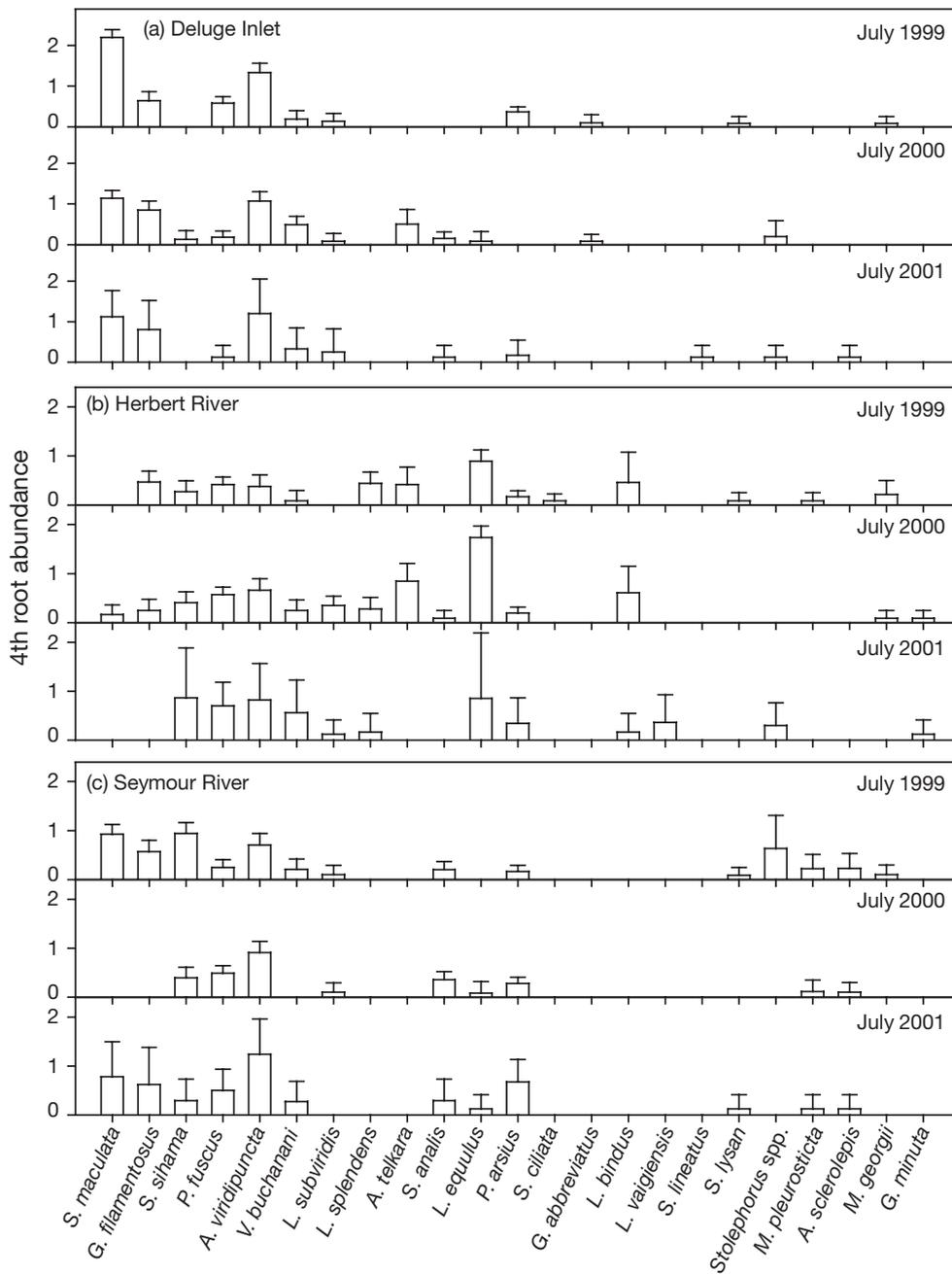


Fig. 6. Mean (4th root transformed) abundances,  $\pm 95\%$  confidence intervals, for species occurring in at least 10% of samples overall: (a) Deluge Inlet, (b) Herbert River, (c) Seymour River

distinct from those in July 1999, July 2000 and July 2001 (Figs. 2 & 3 and 4–6 vs. 7), reflecting high seasonal recruitment in November. Secondly, there were no clear differences among estuaries during November 1999 (Figs. 2, 3 & 7). This was more surprising. It suggests there was little systematic pattern in the variation of larval supply and/or early post-settlement survival at either spatial scale. The fauna was dominated by juveniles, so systematic variation in either of these processes should

lead to different faunal compositions between estuaries. Thirdly, for July samples, differences among estuaries were greater than differences among years (Figs. 2 & 3). In fact, each estuary possessed a composition in July of each year that was different from the composition in other estuaries (Figs. 4 to 6). Not only were there consistent differences among estuaries over time, but the taxonomic compositions in each estuary were consistent over the 3 samples from July. Finally, although there was

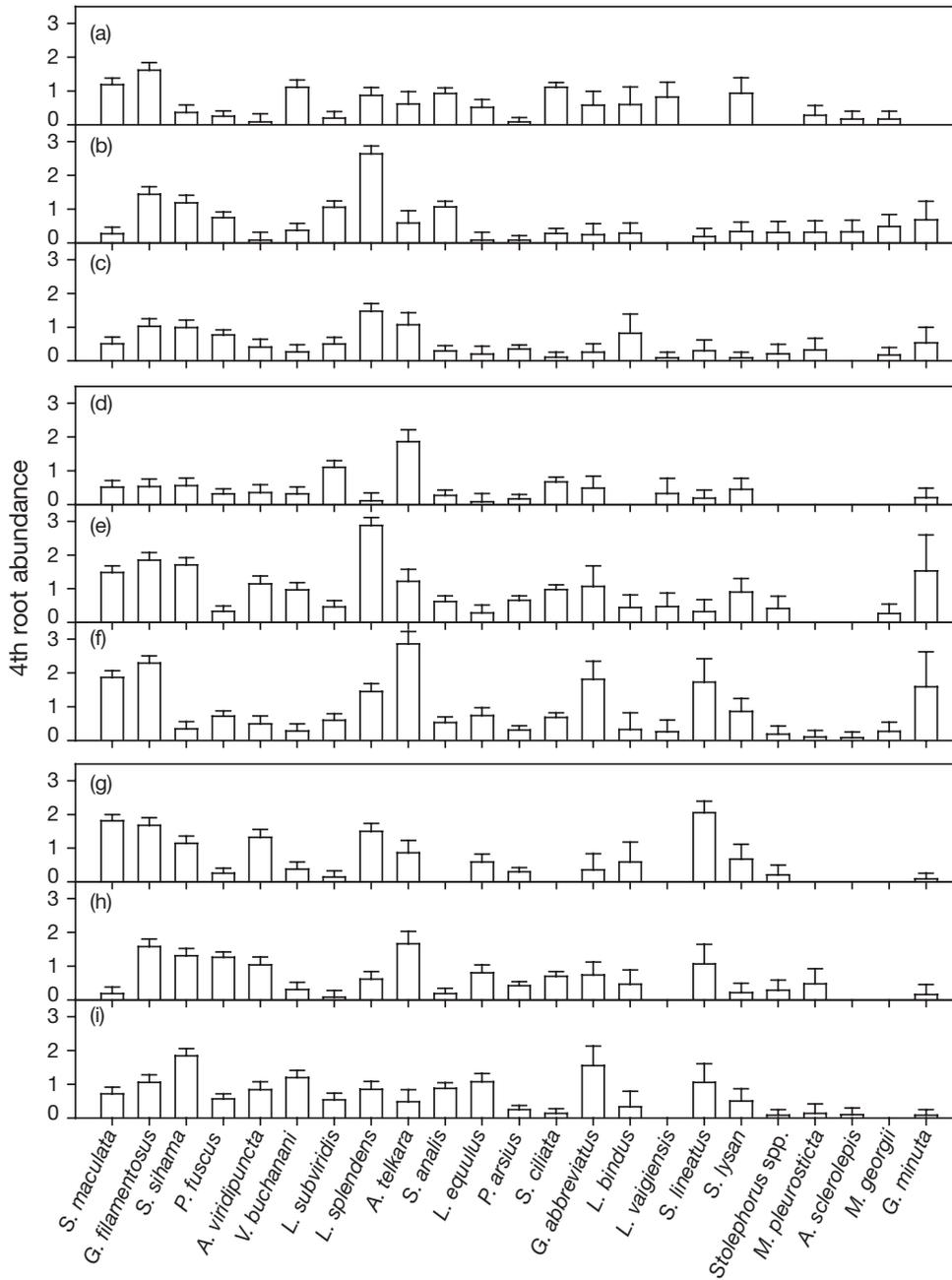


Fig. 7. Mean (4th root transformed) abundances,  $\pm 95\%$  confidence intervals, for species occurring in at least 10% of November 1999 samples: (a) Blacksoil Creek, (b) Haughton River, (c) Morris's Creek, (d) Cassidy Creek, (e) Gentle Annie Creek, (f) Victoria Creek, (g) Deluge Inlet, (h) Herbert River, (i) Seymour River

some indication of between-bay differences, an individual estuary from a single bay was likely to be as much like an estuary from a different bay as like another estuary in the same bay (Figs. 4 to 6).

The patterns apparent in the data are especially pronounced given that bays were defined, and estuaries within bays selected, in such a way as to minimise sources of confoundment. This should have had the effect of reducing among-estuary variability. For

instance, only estuaries with a substantial area of sandy habitat in the lower reaches were selected, and sampling was confined to sandy habitats. Consequently, any differences among the fish faunas of the estuaries due to habitat differences were minimised. Additionally, between-estuary variability relative to variability between bays should also have been reduced. Bays were defined so that factors such as larval supply, climate and salinity regime should have

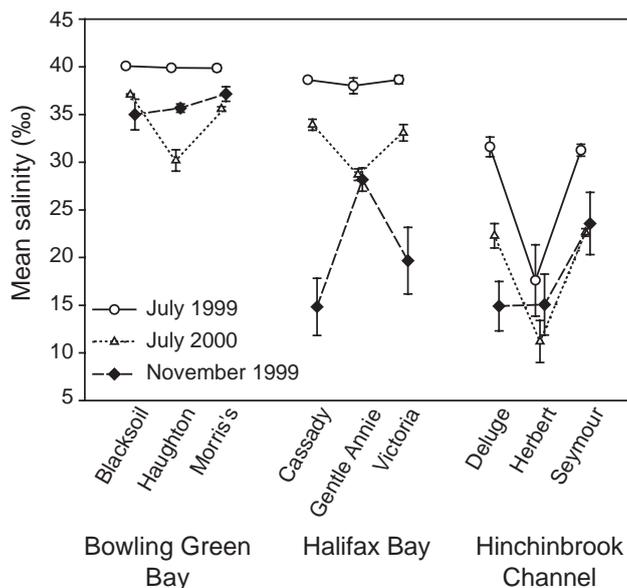


Fig. 8. Mean salinities for 9 estuaries over 3 sampling trips. Error bars are  $\pm 1$  SE

tended to be similar for estuaries within bays, but different among bays. Consequently, given that the sandy habitats sampled represented the vast majority of the habitat in the lower reaches of the study estuaries, it seems that the patterns observed reflect real and consequential ecological features.

Comparing patterns of variation among the full diversity of marine ecosystems is difficult, because for each ecosystem there are logical scales of investigation related to the nature and size of the fauna (Weins 1989). Also, additional scales are added based on the particular aims of each investigation (Schneider 1994a). Consequently, the scales investigated will rarely be exactly comparable. However, in ecosystems containing discrete, natural units, such as estuaries or coral reefs, it seems likely that high variability would be concentrated at predictable scales representing those discrete units. Therefore, characteristic variability at the level of estuaries within this study is not entirely unexpected. What is unexpected is that relatively little variability can be attributed to differences between bays. Faunal variability among spatially close but discrete sampling units, such as the estuaries in this study, is quite different to that seen among coral reef communities in the same area of north-eastern tropical Australia (Hughes et al. 1999), where among-reef variability was low. It is, however, similar to the high among-reef variability seen for coral reef communities in Jamaica (Edmunds & Bruno 1996) and along the Florida Reef Tract (Murdoch & Aronson 1999). Additionally, as with the present study, coral reef communities along the Florida Reef Tract showed much greater variability at the among-reefs scale than

among sectors, a scale that is probably roughly equivalent to the among-bays scale in the present study.

A feature of the present study is that, not only are there consistent differences between estuaries, but the actual patterns of faunal difference were repeated over time, with the same group of species abundant at each estuary from year-to-year (Figs. 4 to 6). It may be that, despite the apparent similarity of habitats among estuaries, the consistent faunal differences between estuaries resulted from unrecognised micro-habitat differences among the estuaries. Beyond this, however, it seems unlikely that the large variability among estuaries within bays, compared to that among bays, can simply be attributed to differences in physical factors. Like kelp forests (Dayton & Tegner 1984), estuaries are not isolated ecosystems, only subject to local physical processes, rather they are influenced by much greater mesoscale physical processes that influence whole regions. Additionally, many physical properties tend to increase continually with distance (Bell et al. 1993). Physical variables that show mesoscale variability or change continually with distance are unlikely to affect individual adjacent estuaries differentially. Some physical factors do show strong local variability however. In the present study, salinity showed substantial variability among estuaries (Fig. 8). However, at any particular time, although the estuaries in some bays showed considerable differences in salinity, estuaries in other bays showed very little variation. If salinity (or a related variable such as flushing by freshwater) was the major factor responsible for the among-estuary variation, this should have led to complex interactions rather than the simple structure of the regression tree model.

There are many biological factors that may be responsible for the characteristic among-estuary variability. It was initially assumed that estuaries within each bay would have a relatively homogeneous larval supply, because of their close proximities and the likelihood that all the estuaries within a bay would be exposed to the same currents. There is no information on larval supply to estuaries in tropical north-eastern Australia; however, around nearby coral reefs larval fish aggregate on at least 2 spatial scales, with patches occurring at a scale of a few metres and at a scale of 10s of kilometres (Doherty 1987). Given that the estuaries in each bay were <20 km apart, it seems likely that on at least some occasions only 1 or 2 of the estuaries would be exposed to a patch of larvae that covered some 10s of kilometres. Thus, the among-estuary variability could be a reflection of unequal larval supply among nearby estuaries. However, this does not seem to be the case in the present study. There was no clear pattern of difference in composition among estuaries during the high recruitment period of No-

vember 1999 that would suggest substantial differences in larval supply. Despite this, by July 2000, the fauna in each estuary had reverted to a very similar assemblage to that in July 1999 (Figs. 4 to 6). This suggests that post-recruitment processes have the greatest influence on shaping the differences among these faunas.

As well as variation in larval supply being a major determinant of abundance, fish faunas may also be substantially shaped by processes occurring at, or subsequent to, recruitment (Clarke 1988, Sale 1988). The abundance of many estuarine fishes is regulated largely by predation (Juanes et al. 1993, Buckel et al. 1999). The occurrences and abundances of roving predators, such as fish (Hixon & Carr 1997) or seabirds (Schneider 1994b, Fauchald et al. 2000), are highly variable in space and time. As a consequence, it is likely that, even if larval supply were equal across all 3 estuaries within a bay, predation pressure would differ greatly, leading to very different degrees of recruitment success and subsequent survival. Thus, differences in predation pressure could result in very different faunal compositions from estuary to estuary. Obviously, detailed knowledge of post-recruitment processes in tropical estuaries is necessary. Indeed, the influence of differential larval supply cannot be discounted without a clear understanding of that process. However, it is clear that either of these processes, as well as a number of other biological and physical mechanisms, could produce the observed among-estuary faunal variation. Despite this, the fact that faunal patterns in the 9 estuaries were repeated from July to July indicates that the driving mechanisms interact with intrinsic features of each estuary to produce a consistent faunal outcome.

## CONCLUSIONS

It is clear that for the estuaries and bays studied, most of the differences in faunal composition were between individual estuaries. Thus, the fish fauna of an estuary was likely to be no more similar to that in a nearby estuary than to the fauna in an estuary 200 km away. However, because this is the first study to investigate spatial scaling in the composition of tropical estuarine fish assemblages, additional investigations in other areas and including other habitat types will be needed to establish if the concentration of variability at the scale of individual estuaries is a characteristic of these ecosystems. If the pattern is general, it suggests that there are major processes structuring tropical estuarine fish faunas focussed at the level of individual estuaries that should be studied and understood (Levin 1992). Clearly, for differences between estuaries to be

apparent, such processes must overprint and modify the general similarities that exist in fish assemblages. General similarities have been noted among faunas of tropical Australian estuaries (Robertson & Duke 1987, Sheaves 1998), and these presumably reflect major structuring factors operating at scales larger than those investigated. Consequently, more extensive studies, covering a greater range of spatial (and temporal) scales, will be needed before the patterns of variability characterising tropical estuarine fish assemblages can be fully understood. Not only do additional spatial scales need to be considered, but the extent to which the pattern of variation detected here is reflected by fish faunas occupying other habitats needs to be determined, as well as the extent to which the pattern is reflected by taxa other than fish. The functional consequences of variability at the estuary-to-estuary level are far reaching. For example, it implies that no single estuary can be assumed to be a control site that can be used as a baseline against which to judge change in an 'impacted' estuary. Rather, a range of control sites would be needed in order to attempt to capture a broad range of 'non-impacted' responses. Better still, coupling this range of control sites with a long time series of pre-impact data from the potentially impacted site would give the best chance of unambiguously detecting any impact.

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