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Interspecific differences in the distribution of adult and juvenile ponyfish (Leiognathidae) in the Gulf of Carpentaria, Australia

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Abstract. The distribution of leiognathids was investigated at 261 sites spread throughout the Gulf of Carpentaria. Eight species, *Gazza minuta*, *Leiognathus decorus*, *L. equulus*, *L. fasciatus*, *L. leuciscus*, *L. smithursti*, *L. splendens* and *Secutor ruconius*, were usually restricted to coastal areas, whereas four species, *L. bindus*, *L. moretoniensis*, *Leiognathus* sp. and *S. insidiator*, were not. Two other species, *L. aureus* and *L. elongatus*, were caught at only one site each. The relationships between size of fish and depth in Albatross Bay were investigated by examining the mean weight and minimum and maximum lengths of different species in 356 trawls. Six of the coastal species showed the common pattern of linear increase in size with depth. This pattern is consistent with the existence of estuarine and/or inshore nursery areas, and supports previous observations of these species. In contrast, three of the widespread species exhibited approximately quadratic relationships between size and depth. This unusual pattern resulted from small fish living in both the shallow inshore areas and deeper offshore areas, and it may reduce competition among the juveniles of the large number of very abundant, coexisting species of leiognathid.

Introduction

The Gulf of Carpentaria is a very large (~400 000 km^2), shallow (<60 m) body of water in northern Australia. It is surrounded on three sides by land, which influences both its hydrology and its sedimentology. Most of the substrata consist of mud and sand, with the muddiest areas occurring in deepest offshore waters and shallow coastal areas in bays and near areas of river discharge (Jones 1987; Somers and Long 1994). It is unlike most coastal areas of Australia in that it does not have a continental shelf.

Depth is the most significant environmental variable correlated with the structure of the demersal fish communities of the gulf (Rainer and Munro 1982; Ramm *et al*. 1990; Blaber *et al*. 1994*b*; Martin *et al*. 1995). Other factors, such as bottom temperature, turbidity, and sediment type are also important. Separating the effects of depth and these other environmental variables is difficult because of their interactions.

Ponyfish, or leiognathids, are among the most abundant fish within the fish communities of the gulf, in terms of both biomass and frequency of occurrence (Blaber *et al*. 1994*b*). Their demersal nature makes them extremely vulnerable to capture by the large fleet of prawn trawlers in the gulf, but they have no commercial value in Australia. Therefore, they constitute a very large proportion of the discards from these trawlers. Leiognathidae is also one of the most diverse families of fish in the gulf, with 15 species, belonging to three genera, occurring there (Jones 1985). Blaber *et al*. (1990*b*) caught 13 species in Albatross Bay and the Embley estuary (see Figs 1 and 2). Despite the importance of these species in the fish community, their ecology and life histories have not been studied in detail.

Previous studies of the gulf's coastal fish communities in Albatross Bay and the Embley estuary (Blaber *et al*. 1989, 1990*b*, 1995; Vance *et al*. 1996), around Groote Eylandt (Blaber *et al*. 1992) and in the Norman Estuary (Blaber *et al*. 1994*a*) provide information on the occurrence of leiognathids in coastal areas of the gulf, including the degree of estuarine dependence of some species. For example, Blaber *et al*. (1989, 1995) concluded that most of the leiognathid species they caught were opportunistic users of estuaries, but that one species appeared to be estuarine-dependent. However, there are no data on the distribution of other species that occur rarely in the inshore waters. The aim of the present study was to identify differences in the life cycles of the leiognathids in the Gulf of Carpentaria by *(1)* interpreting patterns in their gulf-wide distributions, and *(2)* examining the relationships between fish size and water depth in a relatively small area of the Gulf (Albatross Bay) where they are very abundant.

Materials and methods

Gulf-wide distribution

Large areas of the Gulf of Carpentaria were sampled during four cruises of the FRV *Southern Surveyor* in November 1990 (17–63 m depth), 1991 (7–59 m) and 1993 (38–60 m) and February 1993 (34–62 m) (Fig. 1*a*), with a total of 261 trawls. All cruises used similar gear consisting of a Frank and Bryce demersal wing-trawl with a 50 mm stretched mesh cod-end. For details of trawl gear and methods see Blaber *et al*. (1994*b*), an analysis of the fish communities within the gulf using data collected during the survey in November 1990.

Leiognathids were identified following Jones (1985). Total weights of species were calculated for each trawl after sorting the entire catch or, more frequently, a subsample of the entire catch.
Biomass (B; kg ha^{-1}) was estimated from

$$B_{ij} = \frac{C_{ij}}{A_q}$$

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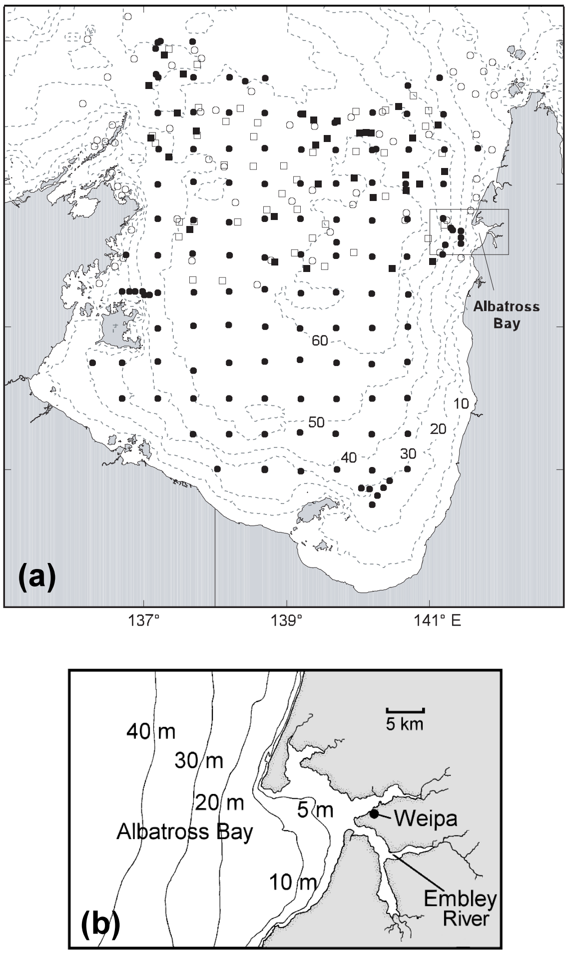

Fig. 1. *(a)* Location of 261 sites trawled during four surveys of the Gulf of Carpentaria: (●) November 1990; (○) November 1991; (■) November 1993; (□) February 1993. *(b)* Location of the depth-related distribution study.

where C_{ij} (kg) is the total weight of species *i* in trawl *j*, *A* (ha) is the swept area of a trawl and *q* is the catchability coefficient. A catchability coefficient of 0.3 was used for all species of leiognathid (Blaber *et al*. 1994*b*). Biomass estimates for each species were plotted on maps and patterns were interpreted qualitatively.

Depth-related distribution in and near Albatross Bay (Fig. 1b)

201 trawls were towed during eleven cruises of the commercial fishing vessel *Jacqueline-D* in August and October 1986, March, August and November 1987, February and November 1988, April 1989, and March 1990, 1991 and 1992; Frank and Bryce demersal wing-trawls with 50 mm stretched mesh cod-end were used in depths of 6–43 m. 15 trawls were towed in February 1988, as above, except that they used 3.6 m prawn-trygear with 50 mm mesh size, in depths from 6–25 m. 37 trawls were towed in August and October 1993 and March, May, July and November 1994 by the commercial fishing vessel *Milana-J*, using Florida Flyer prawn trawls with 50 mm stretched mesh cod-end in depths of 15–25 m. 103 trawls were towed in November 1993 by the FRV *Southern Surveyor* with either a Florida Flyer prawn trawl with 50 mm stretched mesh cod-end or a Frank and Bryce trawl with 50 mm cod-end. Depths of trawls ranged from 15–58 m.

From each trawl, the total numbers and wet weight, and the minimum and maximum standard lengths of fish of each species, were recorded. Data were used only when the total number of fish of a species was greater than five.

Analyses

The relationships between depth and mean weight, minimum length and maximum length were plotted for each species. Regression analyses were performed on untransformed data to help describe the observed patterns (residuals were approximately normally distributed). Simple linear regressions were carried out initially using

$$y = a + bz$$

where *y* is mean weight, minimum or maximum length and *z* is depth. Residuals of the simple model were plotted and a quadratic term (z^2) was added to the model if there was a strong curvilinear pattern. Higher degree terms (e.g. z^3) were not added to the model.

Results

Gulf-wide distribution

Leiognathids were caught at 245 of the 261 sites (Table 1). Of the eight species caught at >10 sites, *Gazza minuta*, *Leiognathus equulus*, *L. leuciscus* and *L. splendens* were usually restricted to the sites closest to the edge of the gulf (Fig. 2), whereas *L. bindus*, *L. moretoniensis*, *L.* sp. (Jones 1985) and *Secutor insidiator*, were not (Fig. 3). Of the species caught at <10 sites each, *L. decorus*, *L. fasciatus, L. smithursti* and *S. ruconius* (two out of three sites), were generally restricted to coastal sites (Fig. 4). *L. aureus* and *L. elongatus* were caught at only one and two sites respectively and could not be assigned satisfactorily to either category.

Depth-related distribution in and near Albatross Bay

Leiognathids were caught in 353 of the 356 trawls undertaken in Albatross Bay; in 220 trawls, =6 species were caught together. In total, 13 species were caught.

Mean weight

The mean weight of *G. minuta*, *L. equulus*, *L. splendens*, *L. leuciscus* and *S. ruconius* increased linearly with depth (Table 2, Figs 5*a*–5*e*). These five species were not caught in depths >50 m, and rarely in depths >40 m; *S. ruconius* was not caught in depths >35 m.

Four species showed approximately quadratic relationships between mean weight of fish and depth (Table 2, Figs 5*g*–5*i*); there were decreases in the mean weights of *L. bindus*, *S. insidiator* and *L. moretoniensis* in depths greater than 30–40 m, but this pattern was not as pronounced in *L. decorus*, which was caught rarely in depths >22 m. The mean weight of *L. decorus* increased linearly up to 22 m depth.

Regressions were not performed on four species, because they were caught rarely: *L. elongatus* was caught only three times, in depths of 50–55 m; *L. sp. was caught 22 times in depths of 17–43 m, but showed no obvious relationship between depth and mean weight;* *L. smithursti* was caught twice at <15 m, where the mean weights were low, and twelve times at 35–45 m, where the mean weights varied from high to low values; on only one occasion were >5 *L. fasciatus* individuals caught, this being in a depth of 21 m with mean weight of 0.067 kg.

Table 1. Catch of leognathids at 261 sites trawled during four cruises in the Gulf of Carpentaria

	No. cruises	No. sites	Depth (m)	Biomass (mean ± s.e.; kg ha^{-1})
Leiognathus bindus	4	221	17–63	1.01 ± 0.16
Leiognathus moretoniensis	4	169	13–63	0.22 ± 0.02
Secutor insidiator	4	72	17–62	0.31 ± 0.14
Leiognathus leuciscus	2	45	10–52	1.47 ± 0.35
Leiognathus sp.	4	40	7–63	0.64 ± 0.21
Gazza minuta	4	32	13–48	0.48 ± 0.22
Leiognathus splendens	4	14	13–46	2.21 ± 0.97
Leiognathus equulus	2	11	18–46	1.67 ± 1.30
Leiognathus decorus	2	8	16–51	0.26 ± 0.19
Leiognathus smithursti	2	8	13–44	1.83 ± 1.27
Leiognathus fasciatus	2	3	22–52	0.17 ± 0.04
Secutor ruconius	2	3	13–47	0.01 ± 0.00
Leiognathus elongatus	2	2	36–42	0.01 ± 0.00
Leiognathus aureus	1	1	37	0.01

Minimum and maximum lengths

The same five species that showed linear increases in the mean weight of fish with depth, *G. minuta*, *L. equulus*, *L. splendens*, *L. leuciscus* and *S. ruconius*, also showed approximately linear increases in both minimum and maximum lengths with depth (Table 3, Figs 6*a*–6*e*).

The same four species that showed quadratic relationships between mean weight of fish and depth, *L. bindus*, *L. moretoniensis*, *S. insidiator* and *L. decorus*, also exhibited quadratic relationships between depth and minimum and maximum lengths (Figs 6*f*–6*i*, Table 3). *Leiognathus decorus* increased in length linearly with increasing depth up to 22 m, beyond which it was caught rarely.

Regressions of depth on minimum and maximum lengths were not performed on *L. sp., L. smithursti*, *L. elongatus* or *L. fasciatus*. Maximum lengths of *L.* sp. did not vary with depth; small fish (<62 mm) were caught in three trawls in depths of 20–30 m, and on the remaining occasions fish were =80 mm. *L. smithursti* was caught only twice in depths <35 m, all being 81 mm at one site and all 90 mm at the other; all fish were longer than these at all but one of the deeper sites. *L. elongatus* was caught only in depths of 51, 52 and 53 m, varying in length from 27 to 59 mm. *L. fasciatus* was caught once at 21 m, varying from 98 to 131 mm.

Discussion

Leiognathus blochii was the only Australian species of leiognathid reported by Jones (1985) that was not captured during the cruises reported in this paper. However, Jones (1985) records this species only in the southern Gulf of Carpentaria and north-western Australia, and as only one cruise in the present study trawled the southern gulf it is not surprising that this species was not recorded.

Coastal and widespread distributions

The results of the gulf-wide study of leiognathids do not define the absolute distribution of each species because trawls were widely spaced in most areas throughout the gulf, especially in the southern half, and the sites closest to the gulf edge were frequently a long way from the coast and in relatively deep water (e.g. >30 m). They are used here to give an overview of the pattern of distribution of each species, in particular to distinguish between those that are restricted to sites closest to the coast, and those that are not.

The restriction of some species to the coast is not explained readily. One reason may be that coastal areas are the shallowest; depth has been correlated with fish abundance in some areas of the gulf. For example, Blaber *et al.* (1990*a*), using data collected during some of the trawls analysed in this study (*Jacqueline-D* trawls), found a quadratic relationship between the transformed catch rates of six species (*G. minuta*, *L. bindus*, *L. decorus*, *L. leuciscus*, *L. moretoniensis* and *S. insidiator*) and depth in Albatross Bay. Blaber *et al.* (1994*b*) reported that depth appeared to be the major factor determining the total biomass of the Gulf fish community. However, they did not investigate the relationship between depth and the distribution of individual species. They also found depth to be correlated with bottom temperature, sediment type and bottom turbidity, and, therefore, depth may not be a direct determinant of the distribution of leiognathids.

Length ranges and mean weights of fish are not as informative as length frequencies, but they constituted the only size-related information available in this study. Single large or small fish can bias length ranges, and the mean weight gives no associated measure of variance in a trawl. When considered together, however, these two pieces of information indicate the general size distribution of fish at given depths. More importantly, consistent changes in mean weight

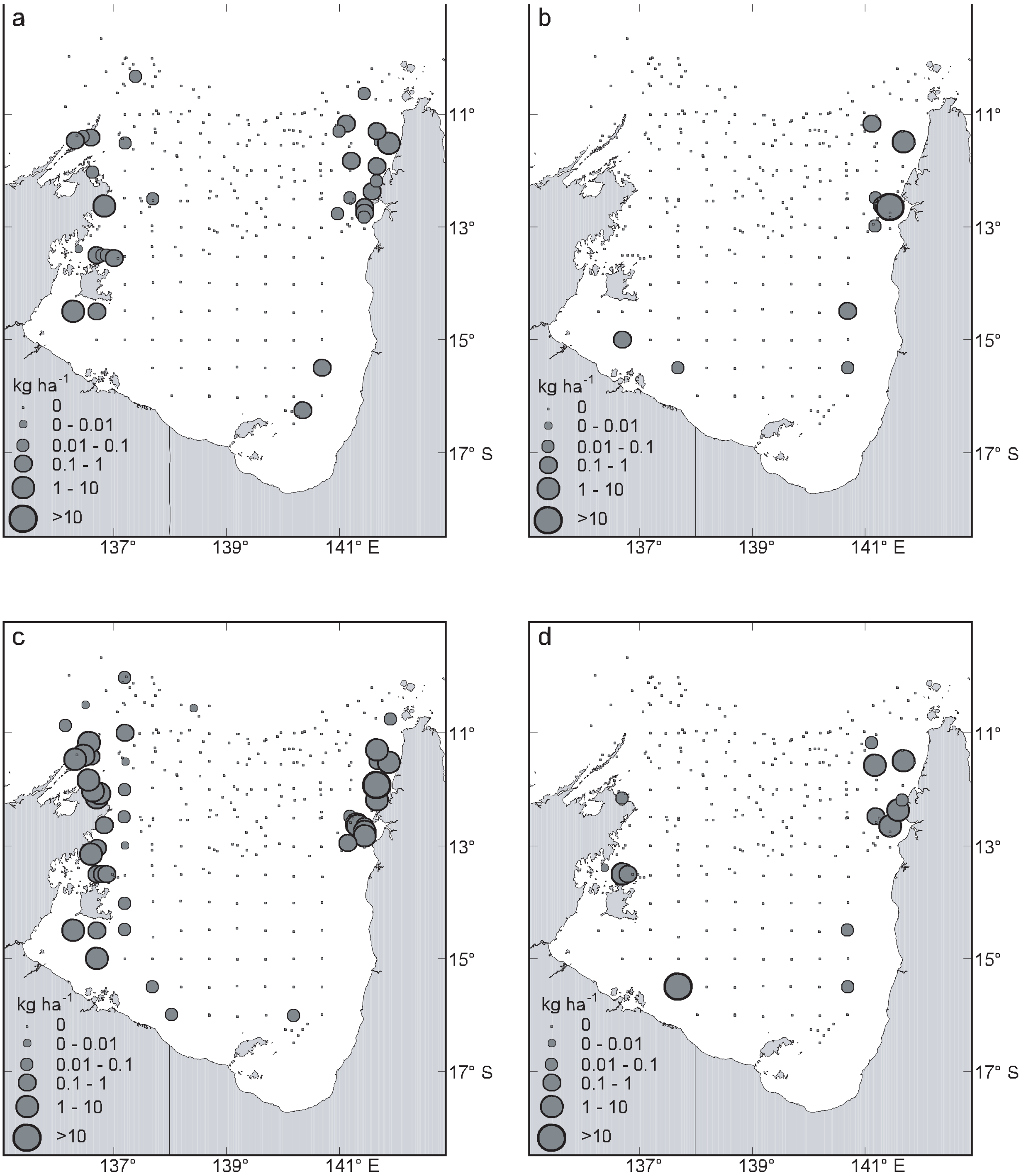

Fig. 2. Distribution of biomass (kg ha^{-1}) of leiognathids caught during four surveys of the Gulf of Carpentaria between 1990 and 1993: *(a) Gazza minuta*, *(b) Leiognathus equulus*, *(c) Leiognathus leuciscus*, *(d) Leiognathus splendens.*

and minimum size of fish with increasing depth support the theory that the smallest fish occur in restricted depths only, rather than being more widely distributed but not accessible to capture in some areas.

The approximately linear increase in size in six species with increasing depth in Albatross Bay is consistent with fish diffusing from nursery areas into deeper waters during ontogeny (MacPherson and Duarte 1991). Small fish of these

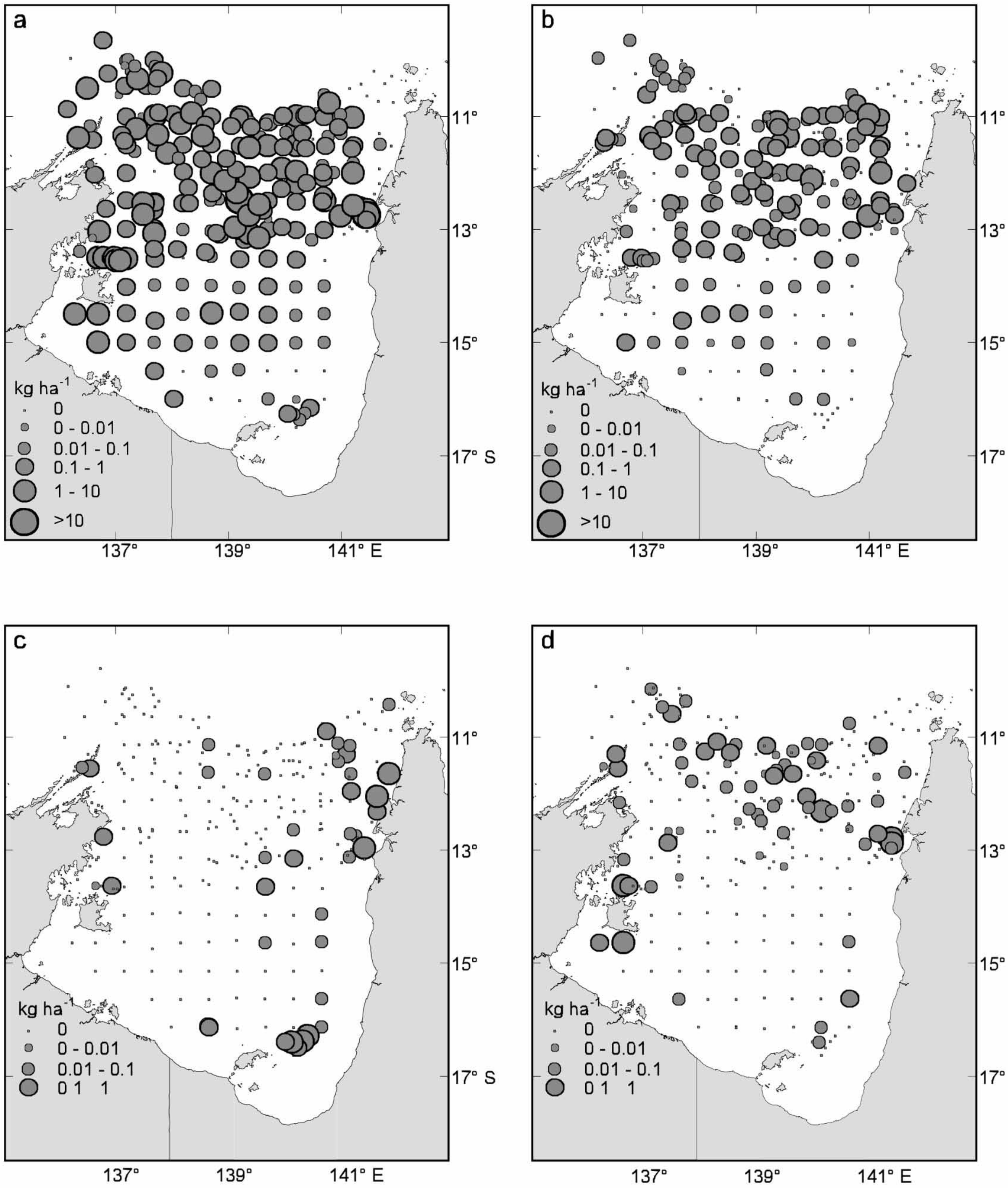

Fig. 3. Distribution of biomass (kg ha^{-1}) of leiognathids caught during four surveys of the Gulf of Carpentaria between 1990 and 1993: *(a) Leiognathus bindus*, *(b) Leiognathus moretoniensis*, *(c) Leiognathus* sp., *(d) Secutor insidiator.*

same six species have been caught in the Embley estuary and the nearshore shallows of Albatross Bay (Table 4; Blaber *et al*. 1989, 1995; Vance *et al*. 1996 and unpublished), although very small *L. leuciscus* (<45 mm) were not caught in any areas. It is not surprising that these species were restricted to coastal sites in the gulf-wide survey, although the distribution of nursery areas does not always constrain the distribution of adult fish. For example, juvenile *Terapon jarbua*, a species

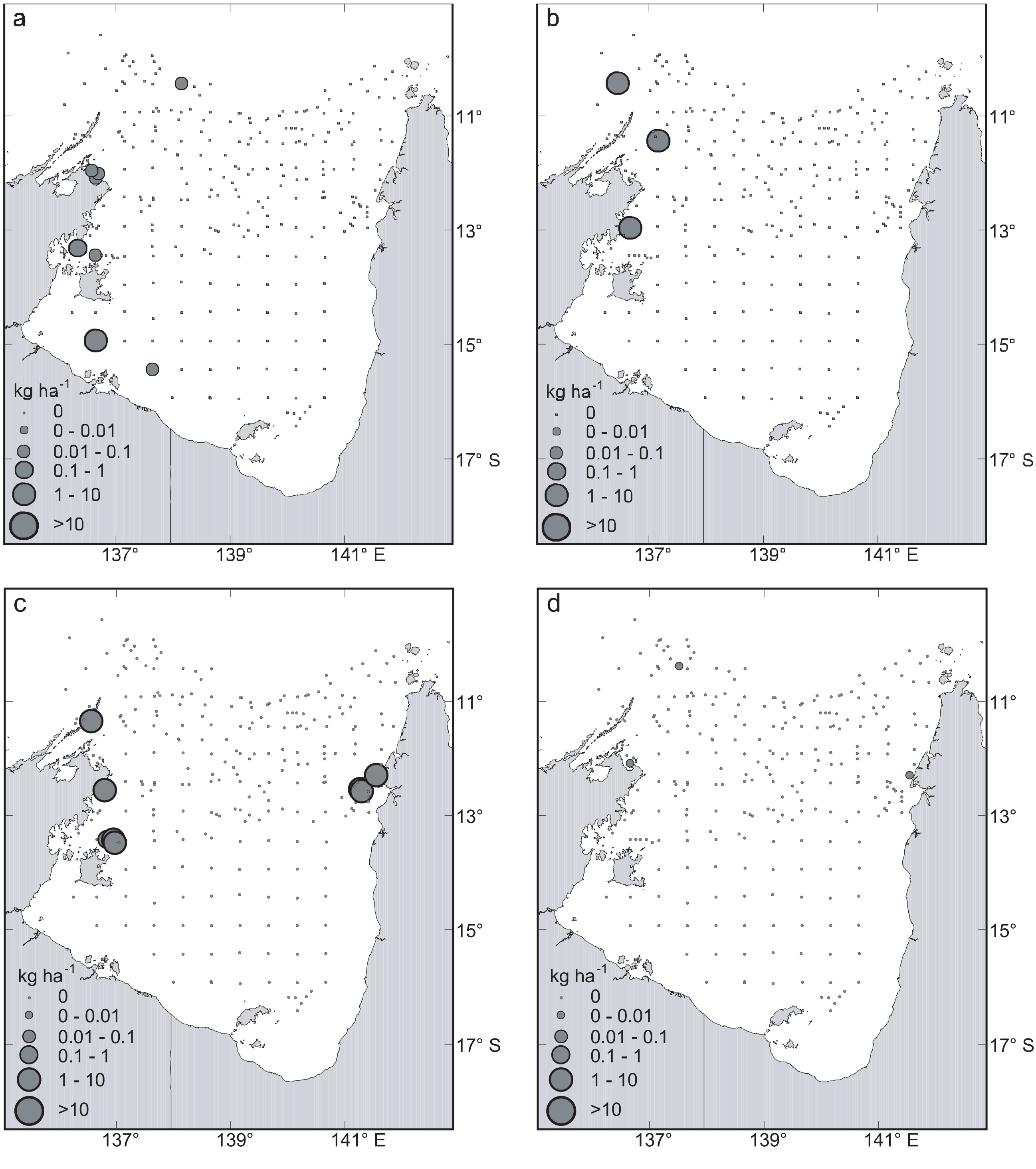

Fig. 4. Distribution of biomass (kg ha^{-1}) of leiognathids caught during four surveys of the Gulf of Carpentaria between 1990 and 1993: *(a) Leiognathus decorus*, *(b) Leiognathus fasciatus*, *(c) Leiognathus smithursti*, *(d) Secutor ruconius.*

that grows to a size similar to leiognathids (<200 mm standard length), were caught by Blaber *et al*. (1989) in the Embley estuary but not the shallow inshore areas of Albatross Bay. Adults of this species, however, occur occasionally throughout the gulf (Blaber *et al*. 1994*b* and unpublished data).

Estuarine dependence and nursery areas

Estuaries, with their large variations in temperature and salinity, are harsh environments for the early stages in the life cycle of fishes. The existence of estuarine stages suggests that the costs associated with living in such harsh environ-

Table 2. Parameters for the regressions of depth *v.* mean fish weight for nine species of leiognathid caught in Albatross Bay
– variable not fitted; ***P<0.0001

	Intercept	Depth	Depth^2	r^2	n
Gazza minuta	0.0099	0.0006	–	0.51***	156
Leiognathus equulus	0.0055	0.0013	–	0.56***	229
Leiognathus splendens	0.0044	0.0007	–	0.56***	274
Leiognathus leuciscus	0.0097	0.0005	–	0.44***	179
Secutor ruconius	0.0032	0.0003	–	0.33***	135
Leiognathus bindus	–0.0044	0.0012	–0.00002	0.40***	256
Leiognathus moretoniensis	0.0068	0.0004	–0.00001	0.16***	174
Secutor insidiator	0.0023	0.0007	–0.00001	0.27***	148
Leiognathus decorus[A]	0.0077	0.0010	–0.00002	0.21***	116
Leiognathus decorus[B]	0.0104	0.0006	–	0.28***	108

[A]Total *L. decorus* caught. [B]*L. decorus* caught in depths ≤22 m.

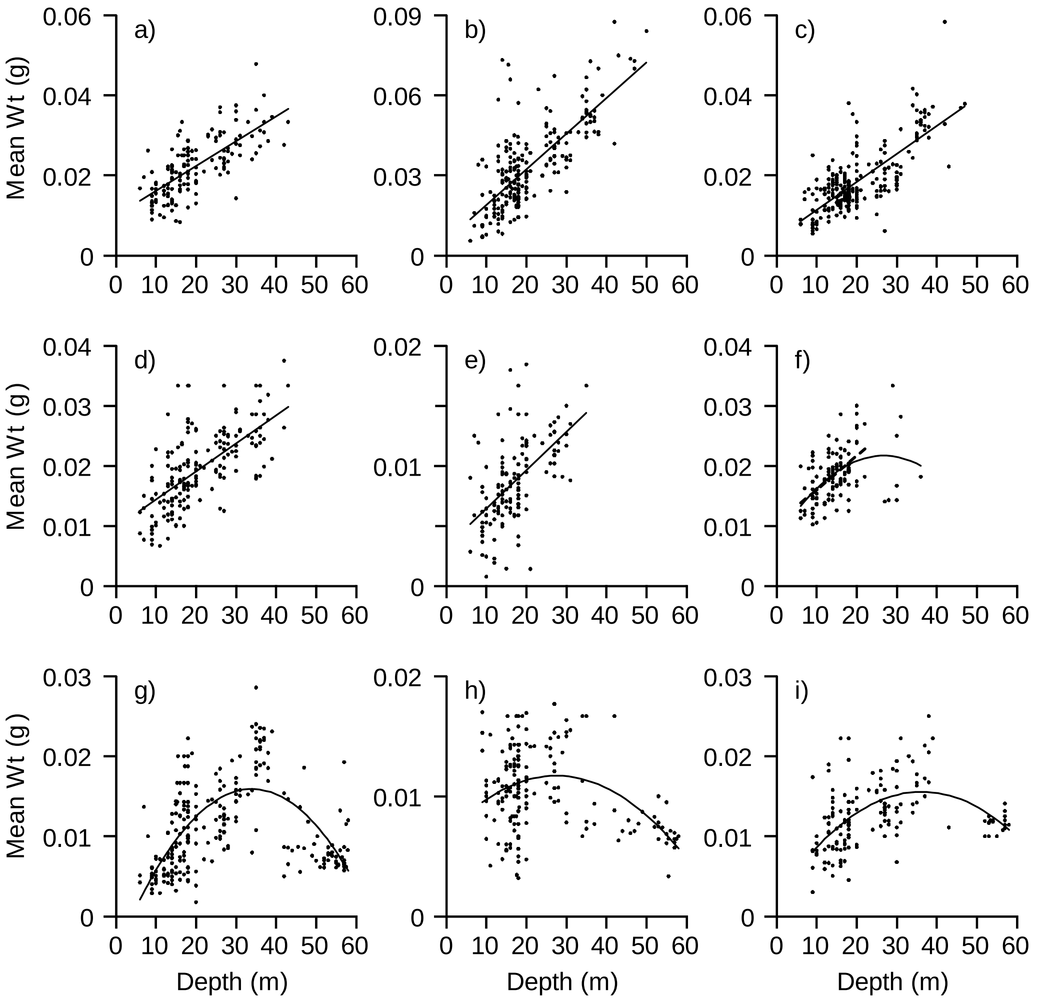

Fig. 5. Plots of depth *v.* mean weight of fish caught in and near Albatross Bay between 1986 and 1993: *(a) Gazza minuta*, *(b) Leiognathus equulus*, *(c) Leiognathus splendens*, *(d) Leiognathus leuciscus*, *(e) Secutor ruconius*, *(f) Leiognathus decorus*, *(g) Leiognathus bindus*, *(h) Leiognathus moretoniensis*, *(i) Secutor insidiator*. Solid lines show significant regressions. Dashed line in *f* shows regression for *L. decorus* in depths ≤22 m.

Table 3. Parameters for the regressions of depth *v.* minimum and maximum lengths of nine species of leiognathid caught in Albatross Bay

Not all fish weighed (Table 2) were measured for length. –, variable not fitted. ***P<0.001; **P<0.01; *P<0.05

	Intercept	Depth	Depth^2	r^2	n
Minimum length					
Gazza minuta	62.905	0.854	–	0.34***	143
Leiognathus equulus	55.379	1.247	–	0.65***	213
Leiognathus splendens	52.785	0.977	–	0.56***	250
Leiognathus leuciscus	65.191	0.483	–	0.16***	161
Secutor ruconius	31.558	1.028	–	0.27***	118
Leiognathus bindus	20.832	2.887	–0.043	0.28***	242
Leiognathus moretoniensis	42.149	1.155	–0.016	0.04*	156
Secutor insidiator	54.365	0.838	–0.010	0.11**	135
Leiognathus decorus[A]	52.402	1.517	–0.016	0.22***	105
Leiognathus decorus[B]	53.114	1.241	–	0.19***	98
Maximum length					
Gazza minuta	89.855	0.546	–	0.20***	143
Leiognathus equulus	94.377	1.279	–	0.27***	213
Leiognathus splendens	79.728	0.634	–	0.29***	250
Leiognathus leuciscus	92.740	0.432	–	0.12***	161
Secutor ruconius	64.171	0.429	–	0.13***	118
Leiognathus bindus	45.576	2.755	–0.042	0.39***	242
Leiognathus moretoniensis	75.728	0.716	–0.015	0.24***	156
Secutor insidiator	66.732	1.316	–0.020	0.23***	135
Leiognathus decorus[A]	79.206	2.204	–0.064	0.16***	105
Leiognathus decorus[B]	89.365	0.520	–	0.06**	98

[A]Total *L. decorus* caught. [B]*L. decorus* caught in depths ≤22 m.

ments are outweighed by the benefits, such as the abundance of suitable food and some degree of shelter from predators (Miller *et al*. 1985). These benefits are not unique to estuaries, and nearby non-estuarine environments may exhibit some similar biotic (e.g. presence of suitable food, low abundance of predators) and abiotic (e.g. high turbidity), leading to their use as nursery areas by a large percentage of coastal marine species (Lenanton 1982; Potter *et al.* 1990; Blaber *et al*. 1995; Blaber 1997). Blaber and Blaber (1980) suggested that juvenile fish of many species were probably attracted to any shallow turbid areas, rather than to estuaries themselves. The coastal waters of the Gulf of Carpentaria, such as Albatross Bay, are highly turbid because of their muddy substratum and relative shallowness. These features, combined with more stable salinities and temperatures than the Embley estuary, partially explain their suitability as nursery areas for some species. The necessity of estuaries in the life cycles of many species has thus been questioned.

Estuarine use and dependence of some Australian leiognathids has been discussed briefly by Blaber *et al*. (1985), who caught three species of leiognathid, *G. minuta*, *L. equulus* and *L. decorus*, in intertidal mangrove forests in north-western Australia but not along the adjacent open shore habitat. Likewise, Robertson and Duke (1987) concluded that juvenile *L. equulus* and *L. splendens* were dependent on mangrove-lined estuaries at several sites along the east coast of Queensland. However, they found both these species, as well as *G. minuta*, *L. decorus* and *S. ruconius*, in nearby seagrass or sandy areas outside the mangrove-lined estuaries. They did not provide comparisons of length ranges of fish from the different areas, but it seems likely that, although largest numbers of most species were caught in estuaries, they were opportunistic users of the estuary rather than dependent users.

Dependence on estuaries of most coastal species in the present study seems unlikely, assuming that the presence of very small juveniles in the nearshore shallows and inshore areas of Albatross Bay indicates their suitability as nursery areas. Only one of the six coastal species, *L. equulus*, was not caught in the coastal shallows (Blaber *et al*. 1995), suggesting that it may be truly estuarine dependent. However, the capture of the smallest individuals of four other species, *L. splendens*, *L. decorus*, *S. ruconius* and *G. minuta*, in the Embley estuary, usually associated with mangroves, suggests that the dependence on estuaries of the smallest stages of these species cannot be ruled out. Unfortunately, differences in sampling methods may affect the conclusions drawn from these data. Within the estuary, nets had very fine mesh (2 mm) (Blaber *et al*. 1989; Vance *et al.* 1996); in the nearshore

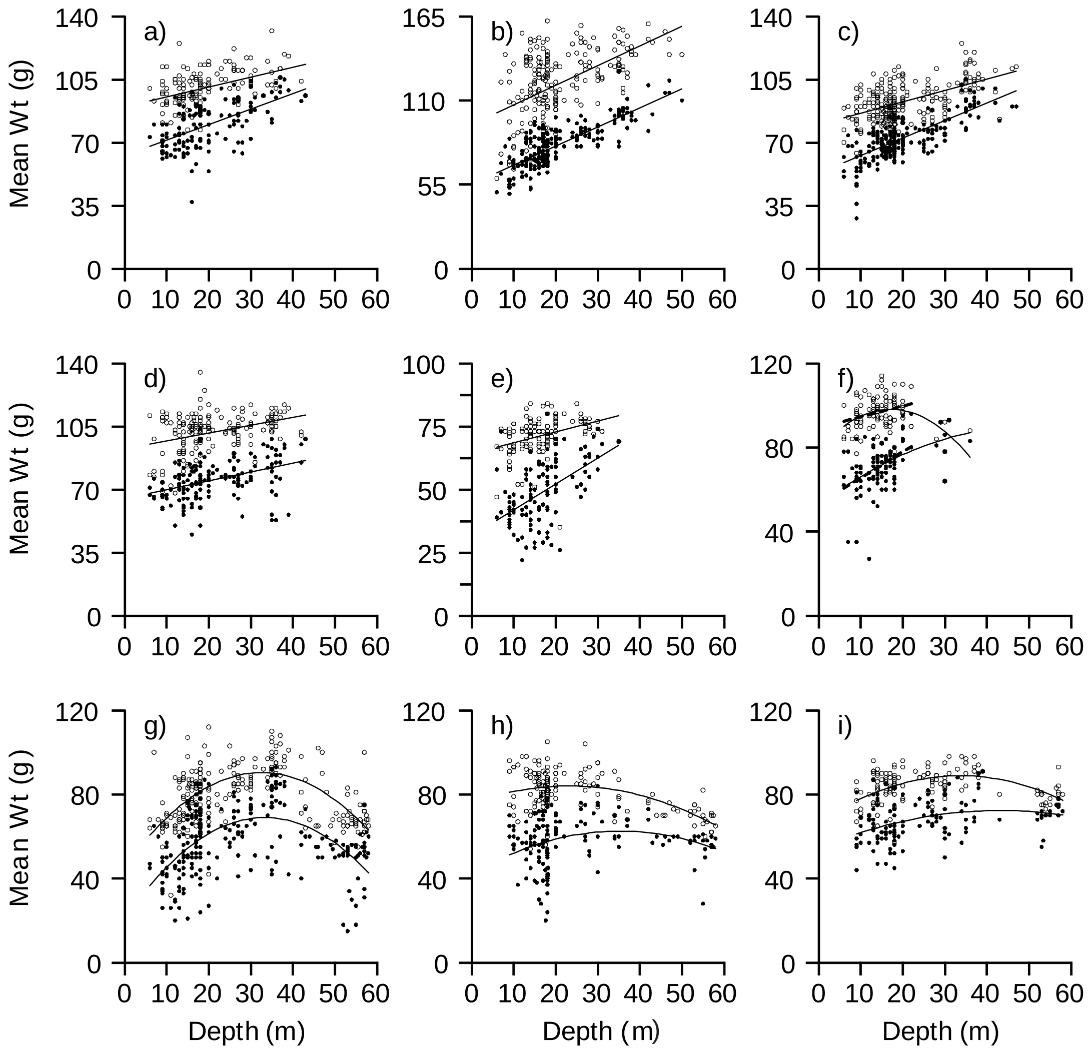

Fig. 6. Plots of depth *v.* (●) minimum and (○) maximum standard lengths (mm) of fish caught in and near Albatross Bay between 1986 and 1993: *(a) Gazza minuta*, *(b) Leiognathus equulus*, *(c) Leiognathus splendens*, *(d) Leiognathus leuciscus*, *(e) Secutor ruconius*, *(f) Leiognathus decorus*, *(g) Leiognathus bindus*, *(h) Leiognathus moretoniensis*, *(i) Secutor insidiato.* Solid lines show significant regressions. Dashed lines in *f* show regressions for *L. decorus* in depths ≤22 m.

shallows of Albatross Bay, the smallest fish were caught in seine-nets with 20 mm mesh (Blaber *et al*. 1995); in the inshore and offshore areas of Albatross Bay, most trawls used nets with 50 mm mesh cod-ends, though some were 25 mm mesh with a 12.5 mm cover (Blaber *et al*. 1989). Because of this bias, the presence of equal-sized small fish in all three areas cannot be excluded.

Offshore nursery areas

In contrast to the linear increase in size of the coastal species as they move away from the coast, three of the four widespread species, *L. bindus*, *L. moretoniensis* and *S. insidiator*, showed an abundance of small fish in both the shallow inshore areas (5–20 m) and deeper offshore areas (>40 m). Very small (<30 mm) *L. elongatus* were also caught in deeper offshore waters, although this species was rare and no pattern to its distribution could be postulated. *Leiognathus* sp. showed no relationship between fish size and depth in Albatross Bay, which, combined with its occurrence away from the coast, suggests it probably has offshore nursery areas. The existence of inshore and/or offshore nursery areas for these five species may be an important factor aiding their distribution throughout the Gulf of Carpentaria.

Juveniles of only one of the four species not restricted to the coast, *S. insidiator*, were caught more than once in the Embley estuary. This species is also the only one of the four that was recorded by Blaber (1980) in the Trinity Inlet system in north Queensland, despite the abundance of the other three

Table 4. Standard lengths (mm) of leiognathids in different habitats of the Embley Estuary and Albatross Bay
Data for inside estuary and nearshore are from Blaber *et al*. (1989, 1995) and Vance *et al*. (1996 and unpublished). Data for inshore and offshore are from the present study

	Inside estuary					
	mangrove	seagrass	sand/mud bank	nearshore (<5 m)	inshore (<20 m)	offshore (>20 m)
Gazza minuta	29–30	70–72		30–47	37–125	64–132
Leiognathus equulus	10–46	21–53	20–58		49–162	80–160
Leiognathus decorus	9–38	20–73	14–60	41–98	27–114	64–109
Leiognathus splendens	22–34	15–51	32–58	23–93	28–112	64–125
Secuto ruconius	10–38	18–32	15–28	21–34	22–84	47–84
Leiognathus leuciscus	48–66	58		55–60	45–135	53–117
Leiognathus bindus			50		16–112	15–110
Leiognathus moretoniensis					15–105	28–104
Secuto insidiator		31–40			44–96	35–98
Leiognathus sp.					55–113	62–119
Leiognathus elongatus						27–73
Leiognathus smithursti					81–90	85–149
Leiognathus fasciatus						98–131

species (*L. bindus*, *L. moretoniensis* and *L.* sp.) in the prawn trawl grounds along that part of the coast (Staunton-Smith, unpublished). Therefore, *S. insidiator* juveniles appear to be the most flexible in their preferences for nursery habitats.

The reasons why only five species appear to use deep waters as nursery grounds, and why juveniles of these species live in the nearshore shallows of Albatross Bay, but not in the Embley estuary, are uncertain. They may be related to where and when different species spawn, physical conditions affecting survival and dispersal of eggs and larvae, behaviour related to avoidance of predation, and the availability of food for early life-stages of the fish (Johannes 1978; Blaber and Blaber 1980; Cyrus and Blaber 1987; Robertson and Duke 1987; Ruiz *et al*. 1993; Martin *et al*. 1995). Somers and Long (1994) reported a difference in the temperature of surface and bottom waters of ~1–2° in 30–40 m depth and 4–5° in depths >50 m. These conditions, or some correlated physical or biological conditions, may affect the suitability of deep water as a nursery area. It is possible that the existence of offshore nursery areas for some species of leiognathid results in decreased competition among the juveniles of the very abundant, coexisting species.

Differences in the life cycles of leiognathids have not previously been studied. Some Australian studies have focused on a great number of species, only some of which were leiognathids, and they have not discussed the species that do not occur in estuaries (Blaber 1980; Blaber *et al*. 1985, 1989, 1995; Robertson and Duke 1987). The only other study to report offshore nursery areas for leiognathids was that of Balan (1967), who caught small juvenile *L. bindus* (35–50 mm total length) in deep waters (>30 m) off the coast of India. Wright (1989) reported that *L. decorus* spawned within a coastal bay in Kuwait, and the juveniles lived in the intertidal parts of the bay, where detached macrophytes provided suitable habitat. Use of estuaries by leiognathids has been reported more frequently. For example, Chua (1973) reported several species, including *L. bindus*, in the Ponggol Estuary, Singapore. He did not, however, state whether these fish were adults or juveniles. Caces-Borja (1975) generalized for 15 species of leiognathid found in the Philippines, stating they spawn outside Manila Bay, that the fry are carried into the bay and live in the shallow waters and that they then move into deeper waters as they grow. Likewise, Jones and Sujansingani (1954) and Day *et al*. (1981) suggested that *L. equulus* spawns in the sea and young fish move into Chilka Lake, India, and South African estuaries respectively. More detailed work on the life cycles of leiognathids is needed. In particular, knowledge of the use of coastal shallows and estuaries by young leiognathids is needed in Asia, where this family has commercial value and where most estuaries are affected by humans.

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