Identifying critical estuarine seagrass habitat for settlement of coastally spawned fish

John R. Ford[1,4,*], Robert J. Williams[2], Ashley M. Fowler[1], Deborah R. Cox[3], Iain M. Suthers[1]

[1]School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, New South Wales 2052, Australia

[2]Aquatic Ecology Research Unit, New South Wales Department of Industry & Investment, PO Box 21, Cronulla, New South Wales 2230, Australia

[3]Water Research Laboratory, School of Civil and Environmental Engineering, University of New South Wales, Sydney, New South Wales 2052, Australia

[4]*Present address:* Department of Zoology, University of Melbourne, Melbourne, Victoria 3010, Australia

ABSTRACT: Identifying and conserving sites with consistently high settlement is necessary for protecting recruitment of coastal fish populations. We investigated the initial settlement patterns of coastally spawned juvenile fish entering 4 temperate estuaries with narrow entrances (<500 m wide) on the eastern coast of Australia. Habitat structure (seagrass cover, blade length and syngnathid density), landscape (patch isolation, perimeter to area ratio and distance to ocean) and hydrological factors (maximum current speed, tidal volume and modelled delivery of passive particles) were investigated as possible explanations for settlement patterns into seagrass beds. One site within Lake Macquarie and 1 site within Smiths Lake were found to have consistently high settlement of 9 coastally spawned taxa over different months and were therefore identified as settlement 'hotspots'. The magnitude of tidal volume, the modelled delivery of passive particles and patch isolation together explained 70% of variation in settlement. Sites of high settlement were characterised as (1) being near to a high-volume channel supplying an abundance of larvae and (2) being isolated from other seagrass patches to concentrate settlement. Monthly variation in settlement, while affecting species composition and total fish abundance, did not alter the relative importance of the identified hotspots, suggesting that these common factors were driving settlement across different species.

KEY WORDS: Estuarine circulation · Larval settlement · Larval and juvenile fish · Hydrodynamic model · Passive particle tracking · Seagrass · Conservation · Essential fish habitat · Passive transport

INTRODUCTION

Many commercial fish spawn in the coastal ocean, with the larvae and juveniles recruiting to estuarine nursery areas, such as seagrass beds (Bell & Pollard 1989, Heck et al. 2003). Among seagrass beds, juvenile fish abundance shows great spatial (Bell et al. 1988, Jenkins et al. 1996, Jenkins & Wheatley 1998) and temporal (Upston & Booth 2003, Smith & Sinerchia 2004) variation, making the identification of key areas a difficult task. Spatially consistent patterns of high juvenile abundance do exist within estuarine environments

(McNeill et al. 1992, Smith & Suthers 2000). These areas may receive high numbers of initial settlers, or be advantageous for growth and survival, or a combination of both (Beck et al. 2001). The identification of such critical habitat of high juvenile abundance, and the physical and biological mechanisms behind them, are a necessary step toward the conservation of estuarine environments and fisheries management (Beck et al. 2001).

Three general spatial models have been offered to explain the distributions of juvenile fish settlement within temperate estuaries: the biological characteris-

tics of habitat (habitat structure model; Bell & Westoby 1986a), the geographical location of the beds within a larger landscape (first encounter model; Bell et al. 1988), and the dominant hydrological regimes within an estuary (passive transport model; Jenkins et al. 1997).

Biological characteristics of seagrasses can influence the structure of fish populations by affecting differential survival and growth rates (Heck et al. 2003). Leaf density (Bell & Westoby 1986a) as well as leaf width (Jenkins & Sutherland 1997) can strongly influence the assemblages of certain fish species. Growth rates of fish can vary between seagrass beds (Sogard & Able 1992), and habitats that facilitate higher growth rates may reduce time spent as smaller, vulnerable juveniles (Levin et al. 1997). These higher survival rates may play a role in the selection of habitat by pre-settlement juvenile fish, explaining spatial variation in numbers of juveniles (Leber 1985, Bell & Westoby 1986a), at the scale of tens of metres (Bell & Westoby 1986b). This model of choice driven by habitat structure variation may be effective on small spatial scales, particularly for specific species, although conclusive temporal studies are lacking.

At larger spatial scales of 100s of metres to kilometres, the geographical location of seagrasses within the landscape may be more important than their biological characteristics (Bell et al. 1988). Rather than actively selecting habitat of more complex structure, juveniles settle into the first seagrass bed they encounter (Bell & Westoby 1986b), assuming that mortality in the water column will be greater than that in seagrass (Bell et al. 1987). Proximity of seagrass to the estuary mouth can influence the abundance of coastally spawned (CS) larvae, leading to higher initial settlement closer to the estuary entrance (Hamer & Jenkins 1997, Hannan & Williams 1998, Brown et al. 2005). Isolation of habitat can play a role in concentrating settlement of epifauna (Roberts & Poore 2006) that seek the nearest available refuge (Russell et al. 2005). Similarly limitation of habitat contributed to concentrated settlement of fish in Aransas Inlet (Brown et al. 2005). In terrestrial systems, however, isolation of habitat patches is well documented to have negative effects on both species richness and colonisation rates depending on habitat types and species motility (Bender et al. 2003, Fahrig 2003). Seagrass landscape studies have focused on the roles of fragmentation, edge effects and patch size on fish (Bell et al. 2001, Jackson et al. 2006), with patches of higher perimeter to area ratio, and therefore greater edge, supporting greater juvenile fish densities and species richness (Jelbart et al. 2006). Under this landscape model, the number of fish initially settling into seagrass is driven by proximity of habitat to the larval source, and the size and shape of the seagrass patch.

Variation in larval supply within estuaries can also be attributed to large-scale movement through passive transport (e.g. Jenkins & Black 1994, Luettich et al. 1999). Passive transport predictions, based on modelled estuarine hydrodynamics, are driven principally by tidal flux and wind-driven flows (Luettich et al. 1999, Cox 2001). Circulation models have been successful in predicting larval transport entering from the ocean to an estuary in order to link larval pathways to the temporal (Jenkins & Black 1994, Brown et al. 2004, 2005) and spatial variation (Jenkins et al. 1997, Luettich et al. 1999, Fowler et al. 2000) in recruitment. The 'passive-transport' approach has been effective on a spatial scale of tens of kilometres within the large open estuary of Port Phillip Bay, Victoria (Jenkins et al. 1997), and the more complex estuaries of Beaufort Inlet in North Carolina (Forward et al. 1999, Luettich et al. 1999) and Aransas Bay in Texas (Brown et al. 2005). Low velocity zones are known to accumulate passive particles (Sammarco & Andrews 1988, Nahas et al. 2003) and in turn produce higher settlement (Chant et al. 2000, Stoner et al. 2001, Brown et al. 2005). Most estuaries along the Australian coastline, however, have small, complex estuary mouths where studies of passive transport are difficult.

We evaluated these 3 models in explaining observed abundances of juvenile CS fish within seagrass beds in 4 estuary entrances on the east coast of Australia. Our focus was at a spatial scale of hundreds of metres (distances among seagrass beds) and on recently settled fish (< 7 d or < 20 mm total length [TL]). Using numerical hydrodynamic models and on-site surveys, the biological structure of seagrass, the geographical location of the beds and the hydrodynamic regimes of the estuary entrance were examined. This study aimed to identify any areas of seagrass habitat that consistently support significantly higher numbers of recently-settled juvenile CS fish, and to determine the relationship of habitat structure, landscape or hydrodynamic characteristics in explaining observed abundances around the estuary entrance. Our goal was to identify particular factors characterising areas of high initial settlement in order to predict critical habitat for management of estuaries.

MATERIALS AND METHODS

Fish sampling. Four estuaries on the central east coast of Australia were sampled between 2003 and 2005 (Fig. 1, Table 1). Three are barrier estuaries with entrained open entrances to the ocean, and one is an intermittently open coastal lagoon (Table 1; see Roy et al. 2001 for estuary classification). All possess a well defined marine tidal delta of contrasting high- and
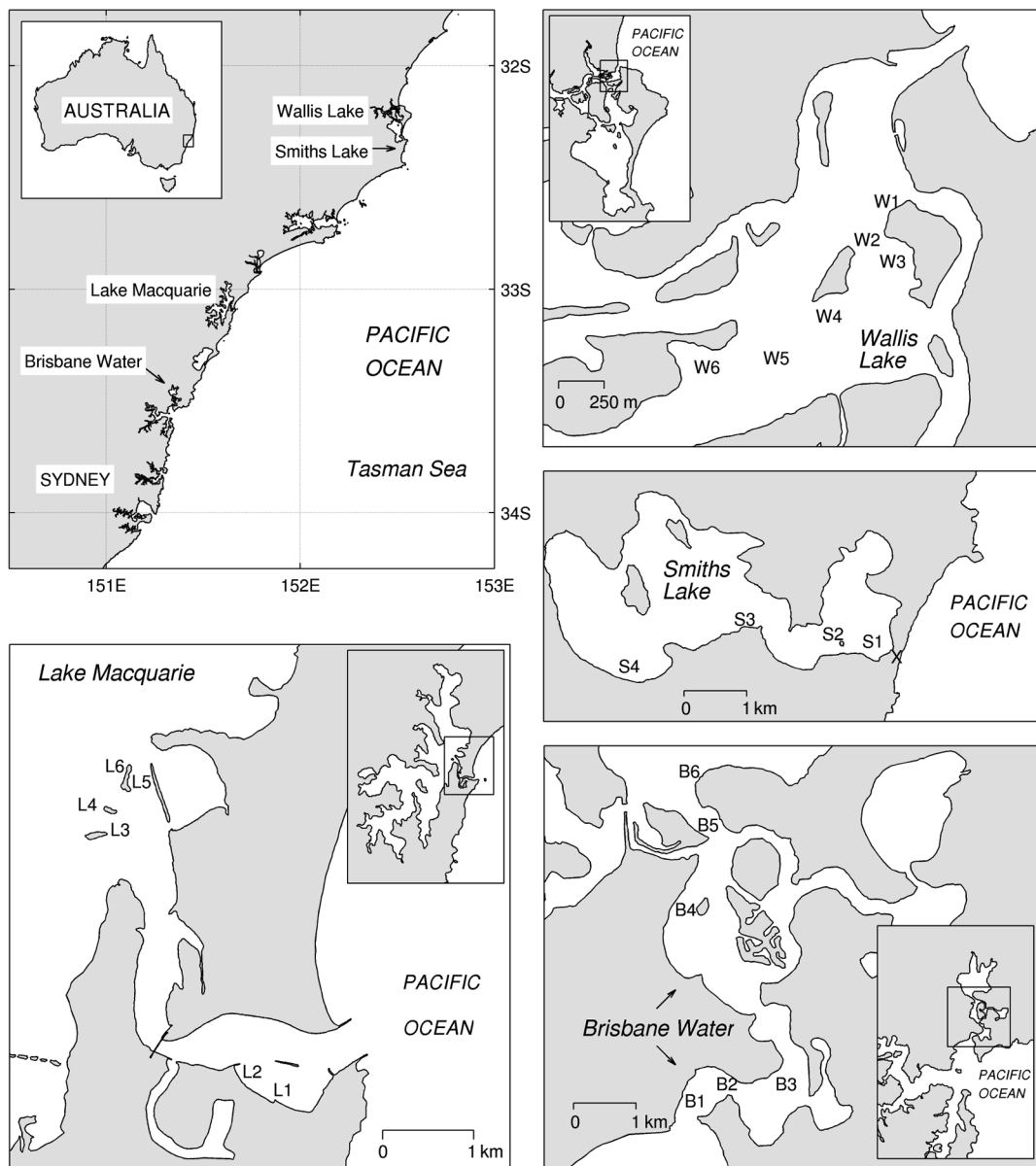
Fig. 1. Location of the 4 study estuaries and position of sampling sites within the estuary entrance. X on Smiths Lake map: intermittently open/closed entrance

low-velocity zones and abundant seagrass *Zostera capricorni* beds.

Six sites in Brisbane Water, Lake Macquarie and Wallis Lake and 4 sites in Smiths Lake were selected based on the presence of seagrass, differing distances to the ocean, optimal depth for sampling and lack of obstructions such as oyster leases. Two replicate beach seine hauls were taken over seagrass at each site. A 2 mm square mesh beach seine (4 m wide and 1.5 m high) was limited to a 2 m wide swath by a cord between each side's dragging pole, such that approximately 18 m^2 were sampled in each seine. Fish larger

than 20 mm were released immediately, along with syngnathids, gobiids and invertebrates. All other fish were anaesthetised in a 1% benzocaine solution, preserved in 5% formalin in seawater and then identified and measured in the laboratory.

Fish were sampled during the day, on the low tide after a night-time flood tide occurring on the new moon. A night-time flood tide is associated with higher abundances of some larval fish entering an estuary (Forward et al. 1999, Trnski 2001) and new moon periods were chosen for their similar tidal conditions. Sampling of the estuaries was not always concurrent and

Table 1. Details of the 4 estuaries

Estuary	Sampling dates	Latitude (°S)	Area (km^2)	Tidal volume (10^6 l)	Seagrass area (km^2)	Tidal range (m)
Brisbane Water	Aug 05, Sep 05, Nov 05, Dec 05	33.31	27.2	21.3	5.5	1.42
Lake Macquarie	Aug 03, Sep 03, Jul 04, Aug 04	33.05	115.1	10.9	13.4	1.16
Smiths Lake	Jul 03, Aug 03, Mar 05	32.21	9.4	0.9	2.1	0.8
Wallis Lake	Jul 03, Aug 03, Aug 04	31.30	86.6	16.6	30.8	1.34

occurred over various months of 2003, 2004 and 2005 (Table 1). All sampling in Smiths Lake was conducted when the estuary was open to the ocean.

Laboratory analysis. Abundance counts were calculated as fish m^{-2}. Due to combined factors of spawning, transport and survival, different species dominate settlement in different months on the Australian east coast (Miskiewicz 1986, McNeill et al. 1992, Smith & Sinerchia 2004). Therefore, the counts of 9 taxa were pooled to provide the number of CS juveniles that had recently settled in the estuary (Table 2). High variance between months and low replication at each site did not allow for appropriate analysis of variance (ANOVA) comparisons on the fish abundance data. To remove these effects, the abundance for each site was converted to a proportion of the total number of fish caught in that estuary in that sampling period (CS proportion). The total for each sampling month in each estuary was therefore equal to 1. CS proportions within each estuary were compared between sites using 1-way ANOVA, with months used as replicates. Data were checked for assumptions and log $(x + 1)$ root transformed where necessary.

Individuals of *Acanthopagrus australis*, *Rhabdosargus sarba* and *Girella tricuspidata* caught in Lake Macquarie, Wallis Lake and Smiths Lake in August 2003 were morphologically staged using the method of Trnski (2003) to determine whether fish were recently settled into seagrass (within 7 d). This technique relies on the concentration and position of melanophores, the development of which was validated with time since settlement.

Circulation modelling. Tidal circulation within the estuary entrances was investigated using numerical models. Lake Macquarie and Wallis Lakes were modelled using 2-dimensional (2D) depth-averaged RMA-10 models developed in previous studies (Cox 1995, 2001). RMA-10 is a finite element model based on the shallow water approximation to the 3D Navier-Stokes and continuity equations. In 2D, depth-averaged applications, the finite element mesh consists of both triangular and quadrilateral elements of variable size, with 6 or 8 nodes located at the corners and mid-sides of each element. The model calculates the current velocity (speed and direction) and water depth at each node.

The hydrodynamic model of Brisbane Water was implemented using Delft3D-FLOW, as part of studies by Cardno Lawson Treloar (2007). Delft3D-FLOW is a finite difference model in which the shallow water Navier-Stokes and continuity equations are discretised on an orthogonal curvilinear grid. The variables are laid out on the grid in a staggered Arakawa-C arrangement, where the water level points are located in the centre of each grid cell, the water depths are at the corners and the velocity components are perpendicular to the faces of each cell. An eddy viscosity is used to specify the horizontal subgrid scale turbulence. A wetting and drying algorithm is included in the model to represent the flooding and drying of tidal flats, whereby nodes may be removed or added back into the flow domain depending on the tide level. All models were calibrated against water level and flow data primarily by adjusting the bed roughness (Manning's coefficient). No numerical model was available for Smiths Lake, a predominantly closed estuary.

The model results from the night-time new moon flood tide of 27 August 2003 (Lake Macquarie and Wallis Lake) and 9 March 2004 (Brisbane Water) were used to characterise hydrodynamic regimes at each of the

Table 2. Nine taxa pooled to calculate the coastally spawned (CS) fish abundances used in site comparisons, with total number of individuals sampled over all months. All taxa are of economic significance in commercial or recreational fisheries

Species	Common name	Family	No. caught
Rhabdosargus sarba	Tarwhine	Sparidae	1073
Girella tricuspidata	Luderick	Girellidae	908
Achoerodus viridis	Eastern blue groper	Labridae	476
Pelates sexlineatus	Six-lined trumpeter	Terapontidae	494
Meuschenia spp.	Leatherjackets	Monocanthidae	294
Acanthopagrus australis	Yellow-finned bream	Sparidae	278
Scobanichthys granulatus	Rough leatherjacket	Monocanthidae	202
Myxus elongatus	Sand mullet	Mugilidae	105
Liza argentea	Flat-tail mullet	Mugilidae	53

fish sampling sites and in the adjacent deeper flow channels. These dates represented typical new moon flood tide events and reflect the different sampling periods in estuaries. Time series of the modelled current velocity and water depth were extracted for each sampling site. Volume fluxes were calculated for transects across the ocean entrance and at each site including its neighbouring channel.

2D particle tracking simulations were used to assess the potential larval pathways and delivery to sites. For Brisbane Water, Lake Macquarie and Wallis Lake, 100 particles were seeded across the entrance to each estuary at the middle of the flood tide (i.e. peak flow). Simulations were stopped at the end of the flood tide (i.e. slackwater), and the location of particles was noted in relation to the nearest sites. Although 3D modelling could be more accurate in tracking particles, taking into account water volume as well as velocity, only 2D applications were available in this study. However, they are considered appropriate for areas of high tidal flows where the water column is well mixed and flow is not significantly driven by wind (Luettich et al. 1999)

Characteristics of sites. Nine environmental variables were used from each site (Table 3) to investigate the biological (seagrass structure), landscape (first settlement) and hydrological (passive transport) models of larval settlement.

Biological: Seagrass cover, blade length and syngnathid density were measured for each replicate at each site. Cover represents the horizontal structure providing juvenile fish with refuge. A Perspex quadrat (35×35 cm) with 50 small holes was haphazardly thrown twice at the location of each replicate seine (i.e. 4 quadrats site^{-1}). Each hole was visually surveyed covering seagrass or bare sand, and the proportion was calculated. Seagrass blade length is the average length of 10 random seagrass blades taken from each quadrat

sample, representing the vertical structure. The abundance of syngnathids, a potential indicator taxon of complex seagrass habitat and a potential flagship group for prioritising seagrass meadows for conservation (Shokri et al. 2008), was calculated per m^2 from those caught in corresponding seine hauls.

Landscape: Landscape factors of site isolation, perimeter to area ratio and distance to ocean were quantified using digital habitat maps (NSW Department of Primary Industries) and the ImageJ graphics program (NIH Image). The isolation index is the proportion of seagrass habitat to open water in a 500 m radius around each site. The perimeter to area ratio was calculated for each sampled seagrass patch. The distance from the estuary entrance to each seagrass site following the deepest channel was calculated using bathymetric maps.

Hydrodynamic: Outputs from the hydrodynamic models were used to calculate 3 factors: maximum flood tide velocity over each seagrass patch, flood tide volume flux over the seagrass patch and nearest channel, and the number of modelled passive particles delivered to within 250 m of the patch. Maximum velocity infers the particle retention rates, where particles are likely to spend longer periods, or 'drop out' in areas of low velocity and also potential disturbance at high flow. The total flood tide volume represents the potential larval supply that passes over or near the seagrass patch. This volume was converted to a proportion of the total flood tide volume entering that estuary to provide comparable data between estuaries of different tidal flux. For each estuary, 100 particles were tracked using 2D simulation to examine the potential delivery of larvae entering the estuary on tidal currents. At the end of the simulated flood tide, we counted the number of particles that were delivered to a 250 m radius around each site. Hydrological data

Table 3. Nine biological, landscape and hydrological factors used to characterise each site

Model	Variable	Unit	How calculated
Biological	Seagrass cover	%	Proportion of seagrass to bare sand
Habitat structure	Seagrass blade length	cm	Average seagrass blade length (n = 40 shoots per site)
	Syngnathid abundance	Fish m^{-2}	Density of Syngnathidae in patch
Landscape	Perimeter to area ratio	Ratio	Ratio of perimeter to area of seagrass patch
First encounter	Patch isolation	Ratio	Proportion of seagrass habitat to open water within a 500 m radius of patch
	Distance to ocean	km	Distance to estuary entrance following major channels
Hydrodynamic	Max velocity over site	m s^{-1}	Maximum velocity over patch on the flood tide
Passive transport	Flood tide volume	Ratio	Volume of water flowing over both patch and in nearest channel, taken as a proportion of total volume entering the estuary
	Modelled particle delivery	%	Percentage of passive particles seeded at the estuary entrance and tracked over a flood tide that were delivered to a 250 m radius of the site at slackwater

were not used for Smiths Lake due to the absence of a model.

The relationship between each of the 9 variables and the proportion of CS juveniles (CS proportion) was investigated using simple linear regression for each estuary separately and for 3 of the 4 estuaries combined. Smiths Lake was not used in this latter analysis due to the absence of comparable hydrological data and because only 4 sites were sampled instead of 6. Data were checked for homogeneity of variance and log $(x + 1)$ or 4th-root transformed where necessary.

The estuary data from 3 of the 4 estuaries (not including Smiths Lake) were included in a multiple linear regression model of CS proportion. Of the 9 site variables, seagrass blade length and seagrass cover were significantly correlated with each other (0.86). Multiple regressions were run omitting first one, then the other, and then both of these variables. This had no influence on the model produced. The model terms were chosen by the lowest value of the Akaike Infor-

mation Criterion (AIC; Akaike 1974). All statistical analyses were conducted using the JMP statistics program (SAS Institute).

RESULTS

Fish abundance analysis

CS fish settlement was highly spatially and temporally variable among and within estuaries. CS settlement density was consistently higher in Smiths Lake and Lake Macquarie than in Wallis Lake and Brisbane Water (Fig. 2). Dominant settler taxa differed among months, but not among estuaries within the same month. Settlement was dominated by sparids and girellids in July and August 2003, labrids and monocanthids in September 2003, terapontids in July 2004 and August 2004 and primarily terapontids and monocanthids in all months of 2005.
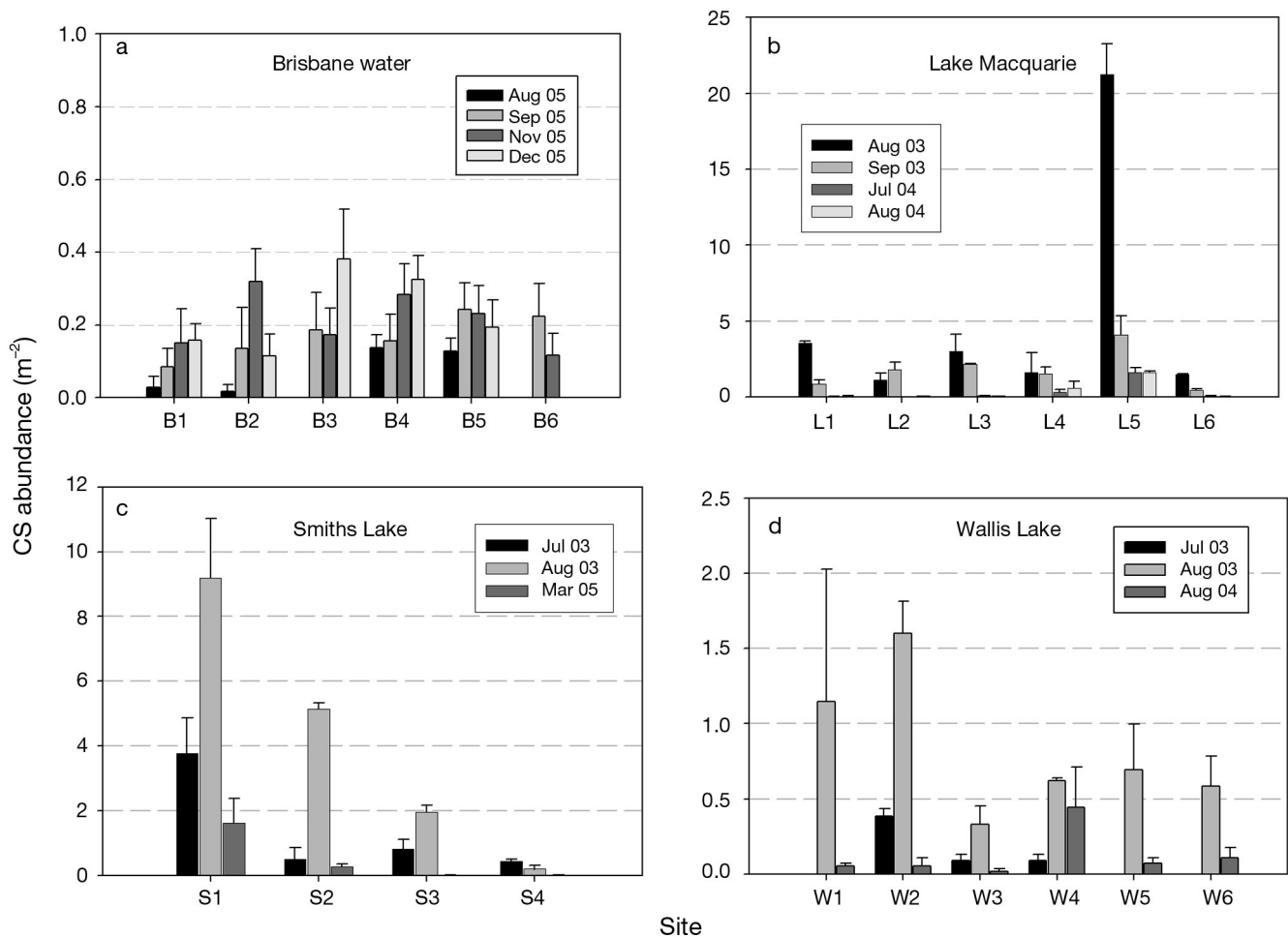

Fig. 2. Abundance of coastally spawned (CS) juveniles sampled in (a) Brisbane Water, (b) Lake Macquarie, (c) Smiths Lake and (d) Wallis Lake. Note the difference in *y*-axis scales and sampling months between estuaries. Error bars are SE
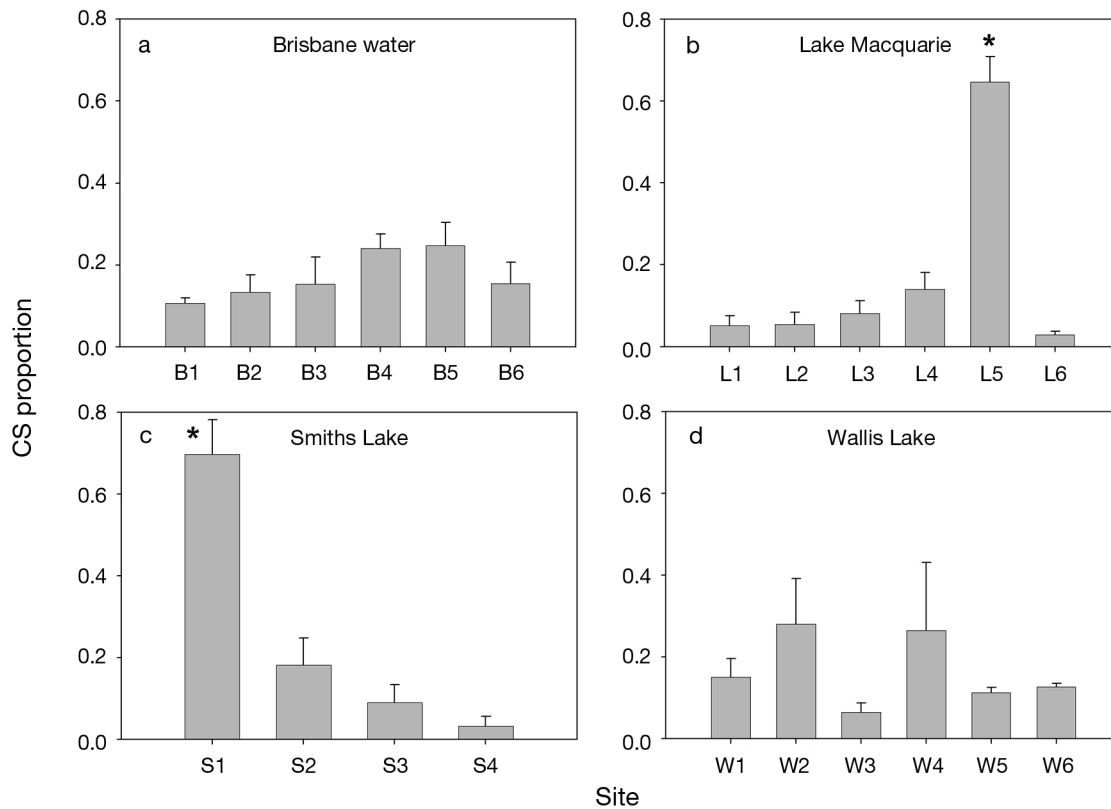
Fig. 3. Average proportion of coastally spawned (CS) fish settlement at each site for (a) Brisbane Water, (b) Lake Macquarie, (c) Smiths Lake and (d) Wallis Lake. Total fish settlement at an estuary in any month was used to find a proportion of this total sampled at each site, so the total for each sampling month in each estuary was therefore equal to 1. *Significantly higher proportion of fish sampled compared to other sites within that estuary (post-hoc Tukey's test, p < 0.05). Error bars are SE

Comparisons of CS proportions showed a significant difference among sites for both Lake Macquarie (ANOVA, n = 6, F = 51.9, p < 0.001) and Smiths Lake (ANOVA, n = 4, F = 12.0, p < 0.001; Fig. 3). In contrast, Brisbane Water showed modest but consistent settlement across sites and months (NS, p = 0.14), while Wallis Lake showed high variance across sites and months (NS, p = 0.20).

Post hoc Tukey's tests showed that 2 sites, L5 and S1, had significantly higher CS proportions than all other sites in their respective estuaries. Lake Macquarie Site L5 and Smiths Lake Site S1 received respectively 43 to 79% and 56 to 85% of total settled fish each month. Proportions of CS settlers at these 2 sites were consistently more than twice the proportion of those at the next most abundant sites within each estuary. Site L5 had the highest settlement densities of any site for 6 of the 9 taxa: *Rhabdosargus sarba*, *Girella tricuspidata* and *Acanthopagrus australis* in August 2003, *Scobanichthys* and *Meuschenia* spp. in September 2003 and *Pelates sexlineatus* in July 2004 (Table 4). Site S1 was similarly representative in its taxa, showing the highest settlement densities for 2 and the second highest for 4 of the 9 taxa.

Table 4. Mean abundance m^{-2} and standard error (SE) of the 9 taxa at the site of highest **(bold)** and second-highest abundance. Note that Site L5 has the highest abundance of 6 of the 9 taxa and Site S1 has 2 of the highest

Species	Sites of highest abundance	Mean density m^{-2} (SE)
Girella tricuspidata	**L5**	**13.6 (0.5)**
	S1	3.7 (1.4)
Rhabdosargus sarba	**L5**	**4.6 (1.6)**
	S1	3.3 (1.1)
Meuschenia spp.	**L5**	**3.2 (1.1)**
	S1	0.7 (0.2)
Myxus elongatus	**S1**	**2.2 (1.5)**
	S2	0.3 (0.2)
Acanthopagrus australis	**L5**	**2.1 (0.5)**
	S2	1.0 (0.1)
Pelates sexlineatus	**L5**	**1.6 (0.4)**
	S1	1.1 (0.4)
Scobanichthys granulatus	**L5**	**1.1 (0.6)**
	L4	0.6 (0.2)
Achoerodus viridis	**W1**	**1.1 (0.8)**
	L4	0.8 (0.4)
Liza argentea	**S1**	**0.9 (0.4)**
	S2	0.2 (0.1)

Rhabdosargus sarba specimens from Lake Macquarie showed the most recent settlement, with 94% estimated to have settled in the 4 d prior to sampling. Wallis Lake specimens were similar, with 87% settling in the previous 4 d. Corresponding patterns were seen in *Girella tricuspidata*, as 99.6% of individuals in Lake Macquarie and 82% in Wallis Lake had settled into seagrass within the previous 4 d.

Site factor analysis

Site factor rankings of the site of highest CS abundance in each estuary are presented in Table 5. The L5 hotspot showed the highest flood tide volume and the most particles settling within a 250 m radius at the end of the flood tide. The S1 hotspot is the most isolated and third-closest to the ocean. Site B5 was also highly ranked in flood tide volume and particle tracking, while Site W2 had the highest perimeter to area ratio.

Four significant predictor relationships with CS proportion were detected using linear regression analysis (Fig. 4). Flood tide volume was a significant predictor of settlement patterns in 2 of the 3 estuaries analysed for hydrological factors, viz. Lake Macquarie (p = 0.033, R^2_{adj} = 0.65) and Brisbane Water (p = 0.032, R^2_{adj} = 0.65). Flood tide volume (p = 0.002, R^2_{adj} = 0.43) and isolation (p = 0.038, R^2_{adj} = 0.19) were also significant predictors for the 3 estuaries when data were combined.

The multiple regression analysis using the lowest AIC produced a model with an adjusted R^2 value of 0.86, incorporating flood tide volume, particle tracking results, isolation, perimeter to area ratio and syngnathid abundance (Table 6). Flood tide volume was the main predictor (R^2 = 0.43).

Circulation modelling

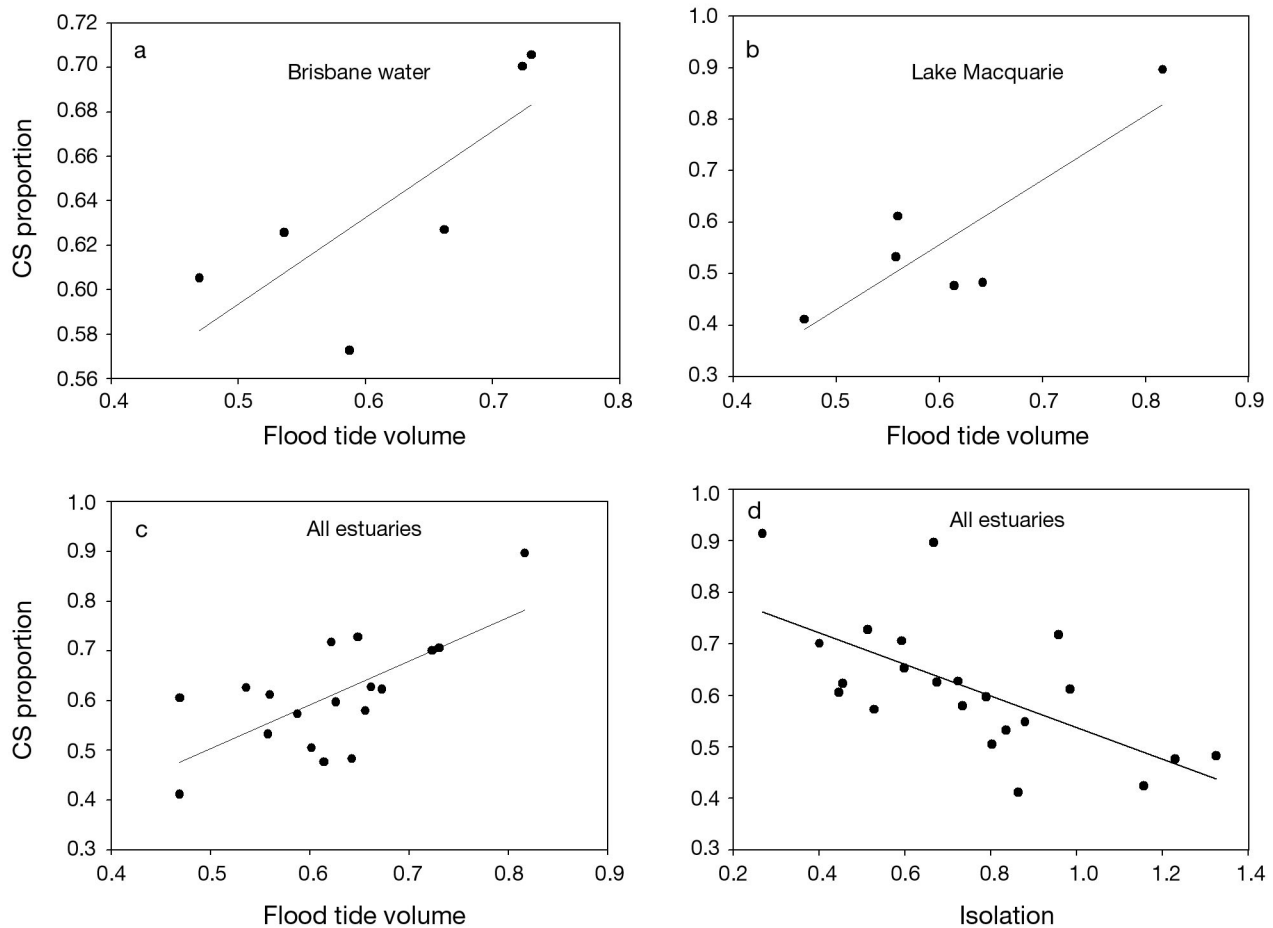In Lake Macquarie, 67% of tracked particles were delivered to within 250 m of a sampled site at the end

Fig. 4. Four significant regressions between coastally spawned (CS) fish abundance and the 9 site factors: flood tide volume in (a) Brisbane Water, (b) Lake Macquarie and (c) all estuaries combined; and (d) isolation in all estuaries combined. All variables and CS proportion were 4th-root transformed

Table 5. Rankings of the site factors for the site of highest fish settlement (coastally spawned [CS] proportion) in each estuary. Rankings are across all 22 sites and are ordered with the lowest numbers predicted to have the strongest positive relationship with fish abundance. CS Prop: coastally spawned fish abundance as a proportion of all fish caught in that estuary; SG Cov: seagrass cover; SG Len: seagrass blade length; Syn Den: density of Syngnathidae; P:A: perimeter to area ratio of patch; Ocean Dist: distance to ocean; Iso: isolation; Max Vel: maximum water velocity over patch; FT Vol: flood tide volume; Part Del: modelled particle delivery

Site	CS Prop	Biological factors			Landscape factors			Hydrodynamic factors		
		SG Cov	SG Len	Syn Den	P:A	Ocean Dist	Iso	Max Vel[a]	FT Vol[a]	Part Del[a]
S1	1	14	3	5	7	3	1			
L5	2	9	14	15	18	20	6	8	1	1
W2	3	15	13	3	1	9	5	16	7	8
B5	5	16	18	7	17	16	7	3	2	4

[a]Only 18 sites were compared for these factors, as Smiths Lake was omitted

of the flood tide: 32% of passive particles ended up within 250 m of L5, 12% within 250 m of L6, 12% within 250 m of L4 and 9% within 250 m of L3. The remainder were farther than 250 m from any site. In Wallis Lake, no particles were within 250 m of any of the sampled sites, with all particles ending up much farther into the estuary at the end of the flood tide. Simulations for Brisbane Water showed only 11% delivered to within 250 m of any site: 9% of particles were delivered to within 250 m of B5, 1% within 250 m of B4 and 1% within 250 m of B3. The majority of particles ended up in the main channel opposite sites B4 and B5, beyond the 250 m radius.

DISCUSSION

Critical seagrass habitat for CS settlement within the estuary entrances studied appears to be a function of the hydrodynamic regime and the spatial distribution of habitat. The role of flood tide volume, or the potential larval supply, explained 43% of variation in settlement across estuaries, where a higher volume of water flux drove higher settlement. Combining this with the particle tracking approach, the 'passive transport' model is in isolation the better approach to explaining the spatial settlement of temperate larvae within the

Table 6. Results of the multiple stepwise regression model of coastally spawned (CS) proportion across all estuaries and the 9 site factors as predictor variables. Abbreviations as in Table 5. Adjusted R^2 value = 0.86

Source	Adjusted R^2	Effect	p
FT Vol	0.43	+	<0.001
Part Del	0.14	+	0.003
Isolation	0.13	+	0.005
P:A	0.10	+	<0.001
Syn Den	0.06	−	0.006

present study. However, the landscape, or 'first encounter' model, was also supported by the significance of site isolation and perimeter to area ratio of patches. The habitat structure hypothesis is all but discounted on the scale of this study.

These findings are reflected strongly in the 2 settlement 'hotspots' found within Lake Macquarie and Smiths Lake. Both sites were supplied with large volume channels and were also isolated patches with large areas of surrounding sand. This interaction of particle transport and habitat limitation was identified previously by Brown et al. (2005), who built upon previous work of Bell et al. (1988) and Jenkins et al. (1997), by comparing modelled particle transport to distributions of settling red drum in Aransas Bay, Texas. Our study incorporates additional factors of habitat structure and landscape and derives similar conclusions about the drivers of larval fish distribution in complex estuaries.

Role of tidal channels as larval pathways

The 2 sites with persistently high settlement, termed 'settlement hotspots', are characterised by their proximity to high-volume tidal channels. Larvae use these strong tidal channels as pathways to access areas of settlement within estuaries (e.g. Jenkins et al. 1996, Stoner et al. 2001); therefore, the position of tidal channels will affect the relative distribution of larvae. Accumulation of fish larvae in stable tidal fronts penetrating estuaries could also result in predictable distributions of larvae on tidal channel paths (Kingsford & Suthers 1996).

In this study, the larval supply is the water originating from the larval source, the coastal ocean. The basis of a strong larval supply in an estuary entrance is therefore a high flood tide volume. Assuming that fish act passively within the current and are evenly distributed through the water column (Jenkins & Black 1994,

Churchill et al. 1999, Luettich et al. 1999), the volume of the channel will represent the numbers of larvae. This approach is applicable for the high channel velocities in this study (>0.5 m s^{-1}) relative to the swimming ability of larvae (<0.13 m s^{-1}; Trnski 2002, Leis et al. 2006). Habitat situated adjacent to a high-volume channel is likely to receive greater numbers of larvae and potentially experience higher settlement.

Flood tide volume can provide an indication of total larval supply, but passive particle tracking can better model when these particles will move past an area of given habitat. As the slack tide approached and tidal current weakened, particles modelled in Lake Macquarie were found overwhelmingly (32%) in the vicinity of the L5 settlement hotspot. Particles were carried past other sites prior to reaching L5, although this occurred at high velocities (>0.5 m s^{-1}). Similarly in Brisbane Water, the flood tide deposited the majority of particles between the 2 highest settlement sites B4 and B5, despite moving past other sites prior to this. The low velocity at the end of the tide allows easier settlement into habitat as the swimming capability is no longer exceeded by local current strength (Trnski 2002).

Similar differences in larval pathways dictated by hydrodynamics are known to drive the spatial variation in recruitment of King George whiting *Sillaginodes punctata* at a scale of tens of kilometres (Jenkins et al. 1997). Larvae behaved as passive particles in the strong tidal channels of Port Phillip Bay before settling out of these currents into seagrass beds. Sizes of such channels, represented by volume flux, will determine the numbers of larvae available for settlement. For example, higher velocity channels carry proportionally more prawn post-larvae to seagrass beds in Northern Australia (Loneragan et al. 1998). Higher recruitment at northern sites than southern sites in Botany Bay was attributed to greater water exchange with the coastal ocean, and therefore larger larval source, in the northern end of the estuary (Steffe 1991, McNeill et al. 1992, Smith & Sinerchia 2004).

Combined hydrological and landscape model

Fish settlement patterns in this study were explained by a combination of hydrological and landscape factors. The importance of larval delivery and tidal volume in the analysis suggests that fish are initially acting passively in the strong tidal currents and potentially engage in active behaviour toward the end of the tidal cycle as currents slacken. Competent fish larvae will attempt to avoid the predation risk associated with open water and settle into any habitat that provides structure and possible protection (Bell et al. 1987, 1988, Jenkins & Wheatley 1998), a scenario supported by our lack of relationship between structural factors and settlement. While seeking refuge on the end of a flood tide, fish are relatively more likely to encounter patches that are both isolated (Brown et al. 2005) and have a high perimeter to area ratio (Jelbart et al. 2006). Both were significant factors in explaining fish settlement in this study. An isolated site will have less competing structure into which fish can settle. Increasing habitat isolation has shown to increase settlement rates (Russell et al. 2005, Roberts & Poore 2006), providing further evidence of settlement into the nearest refuge regardless of structure. The 2 settlement hotspots identified in this study are particularly conspicuous on seagrass landscape maps, as they are surrounded by large areas of open water or shallow sand and were 2 of the most isolated habitat patches in this study (Table 5).

Settlement to the 2 hotspots is represented by all species and groups included in the pooled CS category. The importance of these hotspots was not species specific, heightening their importance as conservation targets for both population management and biodiversity. Species are behaving similarly in their settlement, or behaviour is not playing a detectable role in where these fish settle. Pre-settlement juveniles on coral reefs have the ability to settle using visual (Kingsford et al. 2002, Lecchini et al. 2007), olfactory (Kingsford et al. 2002, Arvedlund & Takemura 2006, Gerlach et al. 2007) and auditory (Simpson et al. 2005) cues, and similar mechanisms are likely to be employed by temperate species locating seagrass habitat. Our study shows that fish were not preferentially settling in areas of more complex structure and were in fact settling at lower densities in areas occupied by syngnathids, an indicator group of high seagrass complexity (Shokri et al. 2008). Behaviour, or 'habitat choice', may still occur at the larval stages of these species; however, the strong hydrodynamic forces influencing the delivery of larvae is likely to override any ability of these fish to effectively detect differences in habitat before settlement.

We therefore propose that the passive nature of larvae in strong tidal currents and the lack of preference for habitat as currents weaken is driving a combined 'passive transport and 'first encounter' explanation for spatial patterns of fish settlement. Fish are delivered on strong tidal currents that slow over the period of the tidal cycle, enabling fish to swim against them and seek the nearest habitat for settlement regardless of structural complexity.

Critical habitat

High settlement of juvenile CS fish in these estuary entrances can therefore be predicted using a combina-

tion of the passive transport pathways, driven by high volume channels, and the relative isolation of that habitat in the surrounding landscape. However, just because fish settle in high numbers in any given patch does not necessarily make it critical habitat of high conservation value. Critical habitat should be identified as an area of habitat that, if lost, will have a persistent negative impact upon the survival of individuals within that estuary. On first glance, the high settlement and isolation of the 2 settlement hotspots detected in this study would suggest that they should be considered critical habitat. Both are surrounded by large areas of deeper water or sand flats providing no structured habitat for settlement. In the case of Site L5, it is the last available area of structured habitat before the channel enters deeper expanses of water. Without this seagrass patch to use as refuge, fish may experience high predation rates in the deeper, low-energy areas while seeking other structure. Site S1, on the other hand, coexists with much 'downstream' habitat and can therefore not be considered critical, potentially acting more like a temporary staging ground. The landscape characteristics and connectivity between habitats with regard to larval pathways must therefore be considered when evaluating critical habitat.

An evaluation of critical habitat must also incorporate the relevance of conservation efforts over time. Seagrass beds are in a continual state of growth and decline, both in extent and density (Meehan & West 2002, Fredriksen et al. 2004), and variation in sedimentation rates, water flow, nutrient availability and sunlight can lead to large temporal changes in seagrass cover (e.g. Shepherd et al. 1989, Larkum & West 1990, Longstaff & Dennison 1999, Cabaco et al. 2008). Seagrass beds that are exposed to high tidal velocities (Fonseca & Bell 1998), shallow water depth (Robbins & Bell 2000) or otherwise exposed to physical disturbance (Fredriksen et al. 2004) can undergo rapid changes and even losses of entire beds. Conditions such as low flow can also have numerous effects, such as greater retention of settled fish (Breitburg et al. 1995) or reduced mortality (Jenkins et al. 1997). Management efforts should therefore focus on identifying more stable beds that are likely to maintain their condition and provide key habitat over time.

No critical seagrass habitat was identified in either Brisbane Water or Wallis Lake as the densities of settlers were either more evenly spread or highly variable between months. Brisbane Water settlement showed little variation between sites or months, with only 1 site in a single month (B5, August 2005) receiving over 30% of settlers in any month. This is explained by the single dominant larval pathway that supplies the majority of sites surveyed. This single dominant channel is fringed by seagrass along the

majority of its length, leading to generalised dispersal along the channel. Wallis Lake has a more complex estuary entrance with numerous diverging channels, but again these channels are all fringed with abundant seagrass beds, both freestanding and associated with extensive oyster leases. Wallis Lake has the largest area of estuarine seagrass in the state of New South Wales (West et al. 1985). There is high availability of settlement habitat along all larval pathways, and hence no consistent high settlement or critical habitat was found.

Management implications

From these examples, it is clear that critical habitat will not occur in all estuaries. The existence of critical habitat could be a sign of high anthropogenic disturbance or poor estuary health, particularly where seagrass loss has fragmented and isolated habitat patches. This is a possible explanation for the existence of the Lake Macquarie hotspot, as the tidal delta has experienced extensive dredging over the past half century. The hotspot lies in the crook of an artificial island created by dredging material. The natural seagrass landscape has been continuously disturbed to the point where this patch is the only suitable settlement habitat supplied by the main (and artificial) channel. It may be possible to engineer such hotspots in degraded estuaries by creating areas of appropriate flow, sedimentation and exposure on the fringes of these channels and create key habitat, either through natural recolonisation (Bryars & Neverauskas 2004), seagrass transplants (Paling et al. 2001, Meehan & West 2002) or the use of artificial seagrass.

Managers of similar estuaries could provide *a priori* protection of locations similar to the hotspots found in this study. The culminating factors of strong larval supply, habitat isolation and low disturbance can identify critical seagrass habitat for the early life stages of CS fish, without the need for expensive and laborious field sampling. Management options could be directed to these areas of critical habitat to maximise their value, by enhancing habitat within settlement hotspots through habitat rehabilitation or the use of artificial seagrass. It could be useful in managing development proposals such as marinas, jetties and bridges in the high-demand foreshores of estuary entrances by regulating development in critical areas.

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