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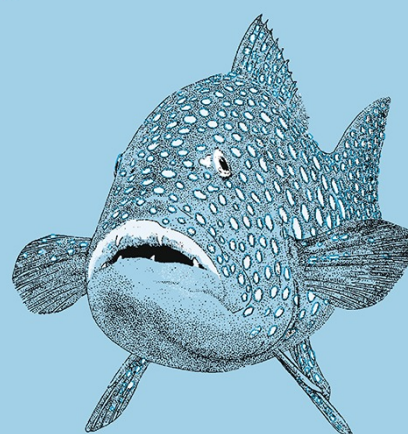
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A review of the biology and ecology of key fishes targeted by coastal fisheries in south-east Australia: identifying critical knowledge gaps required to improve spatial management

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Abstract Knowledge of the population biology, life-history ecology and scales of pre and post-settlement movement of marine species are needed to inform effective conservation management strategies, particularly when spatial information is required for management purposes such as zoning in Marine Protected Areas. This review provides the most current summary from primary and grey literature on the biology and ecology of several coastal fishes of economic and ecological significance in south-east Australia; identifies key knowledge gaps which may impede the development of effective spatial management; and recommends future research directions and methods. Reviewed species are luderick (*Girella tricuspidata*), eastern rock blackfish (*Girella elevata*), yellowfin

bream (*Acanthopagrus australis*), tarwhine (*Rhabdosargus sarba*), snapper (*Pagrus auratus*), red morwong (*Cheilodactylus fuscus*) and eastern blue grouper (*Achoerodus viridis*). The species have a diverse range of life-histories and population traits, and selected parameters were well studied in several species, such as growth (blue grouper, luderick, yellowfin bream, tarwhine, snapper), post-settlement movement (red morwong), and larval ecology (yellowfin bream). However, empirical data on levels of pre- and post-settlement connectivity and real-time movements are not available for most species, and this represents a significant gap for improved spatial management. A multidisciplinary approach incorporating a range of methods including acoustic tracking and telemetry, otolith chemistry, intergenerational markers, and biophysical modelling will provide a more comprehensive understanding of life history parameters, movement and connectivity at scales relevant to MPA planning and monitoring.

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Introduction

Marine organisms are subject to an increasing diversity of stressors, which interact across multiple spatial

and temporal scales (Darling and Côté 2008). Predicting impacts, and recommending appropriate monitoring and intervention strategies is extremely challenging for scientists and resource managers, and is reliant on knowledge of the population biology and ecology, the scales over which marine organisms disperse, and the rate of exchange of individuals among populations (population connectivity) relative to known impacts (Fogarty and Botsford 2007; Jones et al. 2007; Gaines et al. 2010). Empirical data on such factors are available mostly through specific studies on habitat use, patterns of distribution, reproduction, and settlement of larvae (transition from pelagic to benthic life stage) into nursery habitats; and these are often more comprehensively addressed for species of economic importance. Existing studies can also provide insight into how different biological, ecological and physical factors (e.g. pelagic larval duration, larval behaviour, habitat distribution, local oceanography) can interact to determine levels of population connectivity across a range of spatial and temporal scales (Kingsford et al. 2002; Sponaugle et al. 2002). The synthesis of this information is becoming more important due to the increasing use of spatial management to address fisheries and conservation objectives.

Establishing Marine Protected Areas (MPAs) is a specific spatial management tool used throughout the world to protect marine resources from a range of threats (Palumbi 2004). Over the past decade there has been an increase in the number of MPAs along the subtropical and temperate coast of south-east Australia, consistent with the overall objective of establishing a network of MPAs that aims to protect biodiversity and maintain ecological processes (ANZECC TFMPA 1999). This region represents a large ecological gradient extending from southern Queensland to Tasmania, and includes MPAs within the full latitudinal range of the region. Ideally, the design of individual or networks of MPAs (incorporating such things as size, location, spacing, zoning arrangements) would reflect the conservation requirements of the marine organisms within a region (Claudet et al. 2010; Gaines et al. 2010). Those requirements include the patterns of pre and post-settlement movement and connectivity of the key species in a region. In order to maximise the likelihood that the location, size and configuration of MPAs (particularly 'no-take' zones) adequately protect multiple species, information is particularly required on how key habitats are

connected by larval dispersal, whether specific locations act as larval sources, sinks or neither, and what habitats are used by different life-history stages over multiple temporal and spatial scales. While connectivity among populations is recognised as an important component of MPA design, it is not yet routinely incorporated in Australian MPAs (Sale et al. 2005; McCook et al. 2009).

Coastal fishes are a focal group for conservation management efforts and are often a target group for the design, management and assessment of the success of MPAs (Gladstone 2007). They play an important role in the functioning of coastal ecosystems through herbivory, predation, and their role as prey (Kingsford 1998), and many species in the south-eastern Australian region are subject to fishing pressure for food, sport and bait (Rowling et al. 2010). This review synthesises biological and ecological information on several coastal fish species of importance to commercial and/or recreational fisheries along the southeast coast of Australia. The broad objective was to assemble and review all published scientific information (in primary and grey literature) to identify key knowledge gaps for future research which would improve spatial management arrangements in the region. The reviewed species include luderick (*Girella tricuspidata*), eastern rock blackfish (*Girella elevata*), yellowfin bream (*Acanthopagrus australis*), tarwhine (*Rhabdosargus sarba*), snapper (*Pagrus auratus*), eastern blue grouper (*Achoerodus viridis*) and red morwong (*Cheilodactylus fuscus*). These species were chosen as they: are relatively abundant and important components of coastal fish assemblages during their post-settlement stage; represent a diverse range of life histories and ecological traits exhibited by fishes in the region; and are likely to respond to MPA protection due to current levels of fishing pressure. Published and grey literature were reviewed to provide summaries of distribution, habitat use, life-history traits, post-settlement movement and population connectivity for each species. Data from other geographic regions, or from related species, were included when information for south-east Australia was scarce, or when comparisons were considered useful for understanding the biology and ecology of reviewed species. This approach, and the life-history traits covered, is likely to be general to many temperate coastal regions, and therefore broadly applicable to researchers and managers working on MPAs in other temperate regions.

Luderick (*Girella tricuspidata*)

Distribution, abundance, habitat use and diet

Luderick, *Girella tricuspidata* (family: Kyphosidae) are common in shallow estuarine and coastal waters along the eastern and southern coast of Australia and in north-eastern New Zealand (Gomon et al. 2008). In Australia their distribution extends from southern Queensland to South Australia, including northern Tasmania (Hutchins and Swainston 1986). Large fish inhabit estuaries and coastal rocky reefs and are also common around coastal infrastructure such as marinas (Hutchins and Swainston 1986; Clynick 2008). Recruits and juveniles generally occur in shallow estuarine habitats (Morrison 1990; Hannan and Williams 1998), but are sometimes observed in intertidal rock pools on the open coast (Curley pers. obs.). Luderick predominantly form large schools, but can take up a more solitary existence after they reach ~300 mm in length (Morrison 1990). The abundance of large fish on coastal reefs varies at spatial scales of 100's m to 10's of km, and large schools aggregate at specific sites on reefs (Curley 2007). In New Zealand, luderick occur more frequently in barrens habitat than in kelp forests (Anderson and Millar 2004). However, depth is considered to be the most important factor determining abundance patterns within reefs. Luderick are generally more abundant in shallow water of the same habitat, and often utilise the intertidal at high tide for feeding (Kingsford 2002).

Although luderick are omnivores they primarily consume green and red algae, and prefer chlorophytes such as *Enteromorpha intestinalis* and *Ulva lactuca* (Clements and Choat 1997; Raubenheimer et al. 2005). The animal component makes up 12–65 % of their diet and varies seasonally, with the highest consumption of non-algal food occurring during winter (Clements and Choat 1997; Raubenheimer et al. 2005). Fish in the 0+ age-class feed on zooplankton and transition to an adult diet at lengths of 90–100 mm when they move from estuarine to coastal habitats (Morrison 1990). Within estuaries, adult luderick have been found to forage only beneath pontoons where artificial seagrass units were suspended, relative to pontoons without artificial units (Hair and Bell 1992).

Life-history parameters

Luderick become reproductively active at ≥ 2 years of age corresponding to 220–280 mm fork length (FL) for males and 260–320 mm FL for females, with sex ratios sampled from fishery landings in New South Wales (NSW) slightly biased towards females (Gray et al. 2000). The species undertake spawning migrations along the coast of NSW between May and July, travelling in a northerly direction along beaches (Gray et al. 2000). Although these movements have not been quantified, migration is supported by the occurrence of large schools of luderick on coastal reefs in NSW during the winter months (Curley 2007). Luderick are broadcast spawners and are thought to spawn in surf zones or around the mouths of estuaries, daily, at dusk (Gray et al. 2000). They have an extended spawning period in south-east Australia, with a local peak in activity that occurs later at higher latitudes (Smith and Sinerchia 2004). Spawning occurs between July and September in southern Queensland and northern NSW, August–December in central NSW, and October–March in central Victoria (Gray et al. 2000 and references therein).

The pelagic larval duration (PLD) of luderick has not been quantified. However, pre- and post-flexion larval stages have been described, with settlement occurring at around 12–14 mm (Neira et al. 1998). Settlement-stage fish demonstrate complex behaviour such as directed swimming orientation, and are strong swimmers with average near-surface swimming speeds of 12.5 cm or 11.2 body lengths per second (Trnski 2002). Like other estuarine-dependent species luderick probably use estuarine and riverine plumes as navigational cues to locate coastal settlement habitats (Kingsford et al. 2002).

Luderick recruit primarily to seagrass habitats within estuaries (Hannan and Williams 1998; Smith and Sinerchia 2004), although in New Zealand fish settle on shallow estuarine sandstone reefs adjacent to tidal channels (Morrison 1990). Manipulative experiments have shown that luderick settle preferentially to artificial seagrass units suspended in the water column, rather than those located on the seafloor (Hair et al. 1994). In NSW the annual settlement period extends primarily from September to March, with a peak in settlement occurring between early November and late February (Smith and Sinerchia 2004). In central NSW larvae appear in approximately monthly pulses from

September to April, with a peak in abundance in November (Smith and Sinerchia 2004). This periodicity may reflect the timing of spawning or periodicity of advective processes used by marine larvae to enter the estuary (Smith and Sinerchia 2004). For example, monthly periodicity may result from the accumulation of larvae in frontal zones and estuarine plumes (Gray 1996; Kingsford and Suthers 1996) and their subsequent transport into estuaries during flood tides (Smith and Sinerchia 2004).

Formation of annual rings in the otoliths of luderick has been validated with individuals, on average, reaching 170 mm FL after 1 year, 220–270 mm at 3 years, and 310–350 mm at 10 years of age (Kailola et al. 1993; Gray et al. 2000). There is some evidence of differences in growth of luderick across broader spatial scales, with fish in New Zealand growing slower than Australian fish during the first few years (NZ growth rates: 2 years—150 mm FL, 5 years—280 mm) (Morrison 1990). Growth rates of luderick in NSW also vary between sexes in some geographic regions (e.g. Clarence River), although sex-related differences in growth have not been detected in New Zealand (Morrison 1990; Gray et al. 2010). There is a poor relationship between length and age of luderick, but a stronger relationship between otolith weight and age (Gray et al. 2000). The maximum recorded length of luderick is 71 cm FL (Kailola et al. 1993), and maximum recorded age is 24+ years (≤ 560 mm FL) (Gray et al. 2010).

Post-settlement movement

Luderick are considered to be highly mobile as they recruit to estuarine habitats, and move between estuarine and coastal regions as well as along the coast as adults (Morrison 1990; McNeill et al. 1992; Kingsford 2002). After settlement, recruits spend 2–4 months in seagrass habitat before migrating to mangrove habitat or shallow rocky reefs at around 50 mm in length (Middleton et al. 1984; Rotherham and West 2002; Smith and Sinerchia 2004). At sizes >200 mm fish occur in a wide range of estuarine and open coastal habitats (Hannan and Williams 1998; Smith and Sinerchia 2004). In New Zealand fish settle on very shallow reefs within estuaries, move to reefs just inside estuaries at 50 mm and to open coastal reefs at 90–100 mm and ~ 1 year of age (Morrison 1990), and remain on reefs adjacent to estuaries for 1–2 years

before moving to more distant sites. Luderick also undertake pre-spawning migrations along the coast of NSW, with tagged estuarine fish moving distances of >150 km between estuaries (Thomson 1959; Morrison 1990; West 1993a; Gray et al. 2000). Such movements may be the cause of the significant temporal variation in densities of luderick on coastal reefs (Curley 2007).

Morrison (1990) proposed that luderick exhibits intraspecific variation in movement, with some fish displaying high site fidelity and others being migratory. This is supported by tagging data showing that many individuals were re-captured within their release estuary, while others travelled >100 km among estuaries (Thomson 1959; West 1993a; Gray et al. 2000). Preliminary data showing a positive response of luderick to protection within a small coastal MPA ≤ 0.2 km² in NSW also indicates that some individuals may be relatively sedentary (Curley 2007). This bi-modal pattern of movement and unanticipated response of a mobile species to protection within relatively small MPAs has been recorded for other temperate species, such as snapper, *Pagrus auratus* (Attwood and Bennett 1994; Parsons et al. 2003; Egli and Babcock 2004).

Population connectivity/stock structure

There are few data which specifically address population connectivity for luderick. Tagging studies suggest that estuarine populations form a single stock along the east coast of Australia encompassing southern Queensland and NSW (Gray et al. 2000). Limited genetic data also supports this model. Genetic homogeneity of coastal fishes was demonstrated along a ~ 300 km stretch of central NSW using microsatellites (Curley and Gillings 2006; Curley 2007). The geographic distribution of genetic diversity and the high polymorphism found in this study was indicative of high mutation rates, large effective population sizes and high rates of gene flow in this region. Results of tagging and genetic data do not necessarily equate to high levels of population connectivity in luderick. For example, genetic homogeneity may mean that populations are largely 'open' with high exchange of individuals ($>10,000$), or largely 'closed' with sporadic but demographically inconsequential inter-population migration (Thorrold et al. 2001; Hellberg et al. 2002; Mora and Sale 2002). Large scale post-

settlement movements may also be relatively rare and the bi-modal pattern of movement proposed earlier would indicate that populations may be structured at much smaller spatial scales. Luderick in estuaries are known to carry parasitic isopods which could potentially be used to investigate population connectivity (Lanzing and O'Connor 1975).

Eastern rock blackfish (*Girella elevata*)

Distribution, abundance, habitat use and diet

Eastern rock blackfish, *Girella elevata* (family: Kyphosidae) are endemic to Australia and occurs from central Queensland southward to central Victoria, including north-eastern Tasmania (Hutchins and Swainston 1986; Kuitert 1996; Gomon et al. 2008). Rock blackfish populations in Tasmania previously had very restricted distributions; however, an increase in abundance and the presence of gravid individuals have recently been reported and attributed to climate change (Last et al. 2011). The species occurs on coastal and estuarine reefs to depths of 25 m, although they are most abundant in shallow water (<4 m) on exposed rocky shorelines and often move into the intertidal area to feed at high tide (Kuitert 2000; Kingsford 2002). Adults typically prefer surge areas near breaking waves and deep holes adjacent to rock platforms, where they shelter among boulders, caves and crevices (Hutchins and Swainston 1986; Kuitert 1996). Adjacent schools of rock blackfish are typically separated by hundreds of metres to kilometres, reflecting the distribution of suitable wave exposed habitats (Curley unpublished data). Juvenile rock blackfish occur on shallow subtidal reefs and are one of the most abundant species in intertidal rock pools in central NSW (Kingsford 2002; Griffiths et al. 2004). Like adults, juveniles in intertidal pools prefer more wave exposed sites, and exhibit significant variation in abundance between pools, and at scales of 10's m–10's km alongshore (Griffiths et al. 2004).

The diet of rock blackfish consists primarily of chlorophytes and rhodophytes (Bell et al. 1980; Clements and Choat 1997). Despite this they are considered omnivorous as they consume small amounts of animal material, and will take the ascidian *Pyura stolonifera* and crabs when used as bait (Clements and Choat 1997; Kingsford 2002). Rock

blackfish move into the intertidal area to feed at high tide (Kingsford 2002).

Life-history parameters

There are no scientific data on the reproductive biology of rock blackfish, although the species is known to spawn pelagic eggs and it has been suggested by local fishers that large fish move inshore to spawn during spring in NSW (Wilson 1992). There are few data on the early life history of rock blackfish, however, they have a pelagic larval phase and are known to settle into shallow coastal habitat, particularly intertidal pools (Griffiths et al. 2004). A winter-spring spawning season coupled with the relatively high abundance of juveniles (8–42 mm FL) in rock pools in central NSW during spring and summer (Griffiths et al. 2004) suggests that PLD is >30 days; although this has not been validated (Gallahar and Kingsford 1992). Tetracycline experiments have been used to confirm the formation of daily increments in otoliths of juvenile rock blackfish, however, the periodicity of increment deposition in larval fish has not been studied (Gallahar and Kingsford 1992). There are few data on age and growth of rock blackfish, although fish in intertidal pools are known to reach ~100 mm FL in the first year based on size-frequency distributions of specific cohorts (Griffiths et al. 2004). In a tagging study, a 250 mm fish grew 24 mm in 150 days while the average growth of tagged fish >200 mm was 10–15 mm in 50 days (Wilson 1984; NSW Fisheries unpublished data). While maximum recorded length is 60 cm total length (TL) (Gomon et al. 2008) there is no information on maximum age.

Post-settlement movement

Large rock blackfish are thought to be relatively site attached, although this is based on limited data from a volunteer tagging program (Wilson 1984). Over 500 fish were tagged and most of the recaptured fish were caught at the same location where they were released, with the longest distance travelled being 500 m. Limited temporal variability in local abundance of rock blackfish also indicate that the species has a relatively small home range (Curley 2007). High retention of elastomer tags (mean = 77 ± 19 % after 90 days) in juvenile rock blackfish inhabiting rock pools (Griffiths 2002) indicates their potential to

investigate size-related migration of this species from intertidal to adjacent subtidal habitats.

Population connectivity/stock structure

There are no quantitative data on population connectivity of rock blackfish, although the potential for otolith chemistry to elucidate the chronology of conditions experienced during the early life has been examined, with initial results suggesting that some elements will be of limited use (Gallahar and Kingsford 1992, 1996). For example, Sr/Ca in juvenile otoliths did not correspond with the likely thermal history of fish (i.e. transition from pelagic coastal waters to intertidal rockpools) and no direct relationship between temperature and Sr/Ca was found in manipulative experiments (Gallahar and Kingsford 1992, 1996). The development of more sensitive methods for measuring otolith chemistry, however, result in the detection of differences in future studies. Microsatellites developed for luderick (*Girella tricuspidata*) may also be useful for investigating population genetics of this species (Curley and Gillings 2006).

Yellowfin bream (*Acanthopagrus australis*)

Distribution, abundance, habitat use and diet

Yellowfin bream, *Acanthopagrus australis* (family: Sparidae) are endemic to Australia and are distributed from northern Queensland southward to eastern Victoria, excluding Tasmania (Hutchins and Swainston 1986; Hurt et al. 2001; Gomon et al. 2008). The species can hybridise with black bream (*Acanthopagrus butcherii*), and while this was thought to be rare as reproduction in these species is usually spatially and temporally isolated (Rowland 1984), recent studies have shown that hybrids are not uncommon, particularly in regions of greatest sympatry such as southern NSW and eastern Victoria (Roberts et al. 2009). Yellowfin bream often forms large schools on coastal and estuarine rocky reefs, and over sandy areas at reef margins (Kuiter 1996). They also occur within the lower freshwater reaches of coastal rivers (Scandol et al. 2008). Within estuaries yellowfin bream are associated with a wide range of habitats, including seagrass, mangroves, rocky reefs, bare substrates, and

structures such as marinas and jetties (Clynick 2008; Scandol et al. 2008). Small individuals (<20 mm) are more abundant in seagrass habitat than on bare substrates (Gray et al. 1996) and in the seagrass *Zostera capricorni* rather than *Posidonia australis* (Rotherham and West 2002). Fish on coastal rocky reefs are abundant in shallow water (<3 m) and forage in intertidal habitats during high tide (Kingsford 2002). Abundances of yellowfin bream on coastal reefs vary at scales of hundreds of metres to tens of kilometres, and density estimates are associated with large standard errors, due to their patchy distribution and schooling behaviour (Curley 2007).

Yellowfin bream are predominantly carnivorous benthic feeders, with differences in the diet of fish among geographic regions and estuarine habitats reflecting their generalist feeding behaviour. For example, the diet of fish in mangrove and saltmarshes in southern Queensland was dominated by shore crabs followed by terrestrial items (insects, spiders, lizards) (Morton et al. 1987), whereas those inhabiting a tidal mangrove creek in central NSW fed on small fish, polychaetes, decapods, amphipods, benthic copepods, crustaceans and epiphytic algae (Bell et al. 1984). Within estuaries, adult yellowfin bream have been found to forage only beneath pontoons where artificial seagrass units were suspended, relative to pontoons without artificial units (Hair and Bell 1992). There are no published scientific data on the diet of fish within coastal habitats.

Life history parameters

Yellowfin bream reach sexual maturity at 200–240 mm FL (Pollock 1985; Stewart 2008), and possess ovotestes in which the testis and ovary occur in separate zones within the same individual. Ovotestes within an individual change during the transition from juvenile to adult and with season, such that functional reproductive status of individual fish cannot be determined during non-spawning periods (Pollock 1985). Most juveniles become functional males by 2 years of age but a small proportion develop directly into females (Pollock 1985). Extrapolation of such results across the entire biogeographic range of a species, however, is problematic as the mean age at sex change and demographic rates can co-vary even in genetically connected fish populations (Munday et al. 2006).

The species undertake pre-spawning migrations from estuarine to coastal waters along the NSW coast between April and July (Gray et al. 2000), with feeding almost ceasing in spawning fish (Pollock 1984). While Pollock (1982a) found gonads developed to a similar size in all mature fish, ~50 % of the population did not participate in the annual spawning migration. All male fish >2 years of age participated in spawning migrations, with a decreasing tendency for females to migrate with age (Pollock 1984). Non-migratory fish remained in estuarine feeding areas where gametes were eventually resorbed (Pollock 1982a, 1984). The generality of these findings to other geographic areas remains untested. Fish spawn throughout the year along the east coast of Australia in surf zones around the mouths of estuaries, with regional peaks in activity occurring in autumn in central NSW and winter in southern Queensland (Pollock 1982b; Gray et al. 2000; Smith 2003).

Yellowfin bream spawn pelagic eggs which occur over the continental shelf until hatching at ~1.7 mm (Miskiewicz and Neira 1998). Larvae are slightly more abundant between January and April, coinciding with the assumed autumn peak in spawning (Gray 1993; Smith 2003). Larvae exhibit size-related changes in vertical distribution behaviour, and generally become more surface orientated as they increase in size and at ~10 mm are considered neustonic (Smith 2003; Leis et al. 2006). Differences in vertical distribution behaviour exposes larvae of different sizes to different conditions of light, temperature, food and current velocity, which influences growth, survival and dispersal (Leis et al. 2006). Yellowfin bream larvae can also swim in a directional (non-random) manner at speeds which can exceed ambient currents with a maximum near-surface swimming speed of 12 cm s^{-1} (Trnski 2002; Leis et al. 2006). Speed and swimming orientation vary with size, with speed increasing at 1.2 cm s^{-1} per mm, and orientation changing from swimming primarily inshore to parallel at around 10 mm (Leis et al. 2006). Surface swimming and north-east orientation of settlement stage larvae in NSW is thought to maximise encounters with navigational cues such as estuarine plumes to facilitate the detection of estuarine nursery areas (Leis et al. 2006). Within estuaries, surface swimming behaviour exposes larvae to strong wind-driven surface currents which can carry them to a shoreline and appropriate settlement habitat (Trnski 2002). The PLD of

yellowfin bream has not been validated, however knowledge of spawning periods, time of settlement and growth rates suggests that larvae settle after 20–30 days (Pollock et al. 1983).

Yellowfin bream larvae recruit into estuaries over many months, with peak larval abundances in central NSW evident during spring and early summer (McNeill et al. 1992; Rotherham and West 2002). Larvae have been found to be more abundant on night-flood tides within a barrier estuary channel suggesting that they use a particular diel-tide phase to assist movement to settlement habitat (Trnski 2001). Once inside the estuary fish settle into seagrass and mangrove habitats at ~14 mm FL and above (Pollock et al. 1983; Worthington et al. 1992; Gray et al. 1996), with settlement into seagrass beds spatially patchy both within and between estuaries (McNeill et al. 1992; Rotherham and West 2002). Manipulative experiments demonstrate that yellowfin bream settle predominantly to seafloor habitats within estuaries (Hair et al. 1994).

Growth of yellowfin bream varies among geographic regions, with fish in their first year growing to 100–145 mm FL in southern Queensland (Pollock 1982a; Pollock et al. 1983) and 78–100 mm FL in NSW estuaries (West 1993a; Griffiths 2001). These differences may be related to latitudinal variation in temperature as rates of growth after settlement are temperature dependent, with slower growth during winter (e.g. 0.04 mm day^{-1}) and faster growth during the summer months, for example $0.24\text{--}0.67 \text{ mm day}^{-1}$ (Worthington et al. 1992; Griffiths 2001). Females also grow faster and attain a greater maximum length and age than males (Gray et al. 2000).

There is large variation in the lengths of yellowfin bream at any given age (Gray et al. 2000), with fish of legal size (~220 mm FL) in NSW ranging from 2 to 10+ years of age. However, age can be accurately predicted using general and generalized linear models based on a combination of biometric data including otolith weight, length, and sex (Ochwada et al. 2008). The maximum recorded length is 65 cm TL (Kuiter 1996), and maximum recorded age is 22+ years old (36 cm FL), with growth rings validated for all but the first growth increment (Gray et al. 2000).

Post-settlement movement

Yellowfin bream recruits can remain within a single seagrass bed for at least 3–4 months (Botany Bay;

Worthington et al. 1992), after which they move to deeper parts of the estuary and nearshore coastal reefs (Kingsford 2002), although these movements are largely unquantified. Tagging research has shown that juveniles and adults generally moved at scales <6 km, although large-scale movements (10–90 km) were recorded for some adults and appeared to be associated with the migration of fish to, or from surf zone spawning areas (Pollock 1982a). Tag recoveries did not indicate any movement of yellowfin bream beyond a single embayment. In contrast, tagging data from NSW showed that some yellowfin bream inhabiting estuaries undertake pre-spawning migrations up to several hundred kilometres along the coast, move between estuaries, and have a tendency to move in a northerly direction (West 1993b; Pease and Walford 1999; Gray et al. 2000). Despite this, most tagged fish were recaptured in the estuaries in which they were released. Large temporal variation in densities of yellowfin bream on coastal reefs in central NSW suggest that fish regularly move at scales >1 km (Kingsford 2002; Curley 2007).

Population connectivity/stock structure

Levels of population connectivity in yellowfin bream are unknown. Genetic homogeneity has been found for yellowfin bream throughout its described range, with analyses of microsatellite loci indicating high levels of genetic diversity and no genetic differentiation for juveniles separated by distances ≤ 50 km, and adults separated by several 100's km ($F_{ST} = 0.002$) (Roberts and Ayre 2010). Further research is required to assess levels of connectivity among yellowfin bream populations as genetic homogeneity does not necessarily reflect demographically important exchange of individuals. For example, preliminary investigations found significant differences in the otolith chemistry of juvenile yellowfin bream among three NSW estuaries separated by hundreds of kilometres (Gillanders and Kingsford 2003).

Tarwhine (*Rhabdosargus sarba*)

Distribution, abundance, habitat use and diet

Tarwhine, *Rhabdosargus sarba* (family: Sparidae) occur along the east coast of Australia from eastern

Victoria to Queensland and throughout the West Pacific to Japan (Hutchins and Swainston 1986; Scandol et al. 2008). In eastern Australia the species inhabit estuaries and a range of habitats along the open coast, and are generally found in small aggregations to depths of 70 m, sometimes schooling in association with yellowfin bream (Kuiter 2000; Scandol et al. 2008). Juveniles are most common in estuaries and occur in higher abundances in *Zostera capricorni* seagrass beds compared to *P. australis* and *Caulerpa taxifolia* (Rotherham and West 2002; York et al. 2006). Fish are also most common in seagrass beds close to mangrove habitats (Jelbart et al. 2007). Larger fish occur in shallow coastal waters (Smith and Suthers 2000), although the limited available data suggest that tarwhine are not locally abundant on rocky reefs in depths <12 m (Curley 2007). Kingsford (2002) found similar percentages of tarwhine at shallow (42 %), mid (25 %) and deep (34 %) strata on subtidal rocky reefs ≤ 20 m in depth ($n = 101$). Tarwhine are carnivorous, consuming molluscs and benthic invertebrates, including crustaceans and worms (Scandol et al. 2008).

Life-history parameters

Tarwhine from Western Australia are rudimentary hermaphrodites, having both testes and ovaries as juveniles, then transitioning to males or females in which rudimentary remains of ovaries and testes, respectively, are macroscopically undetectable (Hesp and Potter 2003; Hesp et al. 2004b). Preliminary data suggest that populations along the east coast of Australia have a similar reproductive biology (Hughes et al. 2008). Fish tend to move offshore when they become 'physiologically' ready to mature (Hesp and Potter 2003). In NSW, both sexes mature at a similar size, with maturation beginning at ~ 169 mm TL (2 years of age), with 50 % mature at ~ 200 mm FL and all fish mature by ~ 240 mm TL (Hughes et al. 2008). Analyses of fisheries data suggests that sex ratios are slightly biased towards females although this varies seasonally (Stewart 2008). In Western Australia males and females attain sexual maturity at similar lengths (50 % at 170–177 mm TL) in different estuaries, but the age at which fish matured varied among estuaries (2 versus 3 years old for both males and females) (Hesp and Potter 2003).

In NSW spawning occurs during autumn/winter (May–August) on coastal reefs, sheltered bays and lower estuaries, with a peak in activity during July (Hughes et al. 2008; Scandol et al. 2008). Spawning in Western Australia occurs later, during winter/spring (July–November), with fish spawning multiple times throughout the season; for example, fish may spawn 45 times at intervals of 2.7 days (Hesp and Potter 2003; Hesp et al. 2004b). Females of 180–260 mm are estimated to have batch fecundities of about 4,500–12,400 eggs and potential annual fecundities of 204,300–557,500 (Hesp et al. 2004b). Spawning occurs just prior to strong ebb tides which is likely to assist the transport of eggs out of the estuary into coastal waters (Hesp et al. 2004b).

Tarwhine eggs hatch at <3 mm and early development occurs in offshore waters (Neira et al. 1998), with larvae most abundant in subsurface waters from January to April (Smith 2003). Postflexion larvae have been found to be more abundant around fish attraction devices than in open water habitat (Druce and Kingsford 1995). The PLD of tarwhine has not been validated. Settlement-stage fish are likely to have some control over dispersal as they can swim faster than ambient currents within estuaries and have an average near-surface swimming speed of 6.4 cm or 6.5 body lengths s^{-1} (Trnski 2002).

Tarwhine settle at 10–15 mm TL (Miskiewicz and Neira 1998; Smith and Suthers 2000; Hesp et al. 2004a) favouring vegetated estuarine habitats along the east coast of Australia, and unvegetated habitats along the west coast (McNeill et al. 1992; Smith and Suthers 2000; Hesp et al. 2004a). Settlement into nursery areas occurs between June and December off eastern Australia (Hannan and Williams 1998; Miskiewicz and Neira 1998; Smith and Suthers 2000) and August to October in Western Australia (Hesp et al. 2004a), and is temporally and spatially patchy. For example, on the central NSW coast settlement of tarwhine occurs in distinct pulses during winter/spring with settlement commencing in May, peaking in July and ceasing in October (Smith and Suthers 2000), and substantial variation in the abundance of recruits among *Z. capricorni* seagrass beds has been documented (McNeill et al. 1992). The specific factors governing settlement are unclear, with fish settling on flood tides in Western Australia, but patterns in NSW suggest that settlement is not limited solely by spawning times, tides or behaviour and may be

influenced by additional factors such as seasonal coastal winds (Smith and Suthers 2000).

Early growth of fish is rapid with fish reaching 80–90 mm in 7 months in Western Australia (Hesp et al. 2004a), with a single opaque zone laid down annually in otoliths (Hesp et al. 2004a; Hughes et al. 2008). Growth of recruits is temperature dependent, with slow growth during winter (~ 0.02 mm per day) compared to the warmer months where growth is ~ 0.31 mm per day (Worthington et al. 1992). Both sexes grow at similar rates during the early stages, with 1 year old fish reaching 111 mm in NSW and 108–125 mm in Western Australia (Hesp et al. 2004a; Hughes et al. 2008). Fish in NSW achieve 160–210 mm FL in the first 2 years, and 240 mm in 5 years (Hughes et al. 2008). Grow rate then slows to ~ 30 mm per year after fish reach 200 mm TL (Stewart and Hughes 2008). Growth rates of larger fish are similar in NSW and Western Australia (Hughes et al. 2008). The maximum recorded length of tarwhine is 45 cm TL (Kuitert 1996), and maximum recorded age is 16.5 years (27.6 cm FL) in NSW (Hughes et al. 2008). Overall, tarwhine in eastern Australia are more similar in growth rate, maximum size/age, and reproductive biology to fish from Western Australia than tarwhine from other parts of the world (Hughes et al. 2008).

Post-settlement movement

Spatial and temporal variation in abundance, size and age of tarwhine suggest that fish move from shallow nearshore waters to offshore deeper waters as they increase in size (Hesp et al. 2004a). In Western Australia, tarwhine move from unvegetated habitat to *Posidonia* seagrass at ~ 40 mm, and from sheltered to exposed nearshore waters at ~ 90 mm TL, with all fish >5 years found exclusively in the latter habitat (Hesp et al. 2004a). Tarwhine also move among similar habitat types within estuaries. For example, variation in abundance of recruits 10–25 mm standard length (SL) within seagrass suggests that fish move between seagrass beds separated by up to 20 m (Upston and Booth 2003). There are no published tagging data for tarwhine which elucidate scales of movement in coastal waters.

Population connectivity/stock structure

There are no data on levels of connectivity among tarwhine populations. Furthermore, it is difficult to

postulate on population connectivity due to poor knowledge of scales of dispersal during pre- and post-settlement life stages. Otolith chemistry is a promising tool for investigating population connectivity of tarwhine in NSW, with significant differences in juvenile otoliths chemistry among groups of estuaries indicating that the nursery area of adult fish could be determined by examining the juvenile portion of adult otoliths (Gillanders and Kingsford 2003). This would allow determination of connectivity between estuaries and open coastal populations, including distances that fish have moved from their settlement estuary and the number of estuaries that contribute to adult populations (Gillanders and Kingsford 2003).

Snapper (*Pagrus auratus*)

Distribution, abundance, habitat use and diet

Snapper, *Pagrus auratus* (family: Sparidae) are widely distributed throughout subtropical and temperate continental shelf waters of the Indo-West Pacific, Japan, Indonesia, southern Australia and New Zealand (Henry and Gillanders 1999). Snapper occur throughout Australia from central Queensland southward to central Western Australia, including northern Tasmania (Hutchins and Swainston 1986). Recent data suggests that snapper have increased in abundance and expanded their range in eastern Tasmania since the late 1800s (Last et al. 2011). Adult snapper aggregate over rocky reef habitat in shelf waters at depths of 20–60 m, however they can occur to depths of 200 m (Henry and Gillanders 1999). Juvenile snapper are abundant in estuaries, on shallow coastal rocky reefs and sand habitats adjacent to reefs (Henry and Gillanders 1999; Ross et al. 2007). Most fish observed on shallow subtidal reefs in central NSW are juveniles and sub-adults (7–14 cm SL) and are found at depths of ≥ 4 m associated with barrens, sponge habitat or the sand-reef interface (Curley 1998; Kingsford 2002). Significant small-scale (1 km) spatial variability in abundance of juvenile snapper (<3 years old) has also been found over different soft-bottom substrates in New Zealand with fish preferring mud, rather than muddy sand with a significant percentage of shell (Francis 1995). It was also hypothesised that the presence of fish in other 'marginal' habitats was the result of late settling

snapper being competitively excluded from preferred sites. No consistent depth-related trends in the abundance of juvenile snapper have been detected over the range 10–30 m in these habitats (Francis 1995). Snapper prefer habitat patches and areas of higher structural complexity, for example beds of horse mussels, *Corallina* turf, sponges, sea squirts, pits and burrows (Kingett and Choat 1981; Morrison et al. 2008). Juveniles are almost always observed close to, or on top of these types of structures which are thought to provide shelter from predators, as well as good foraging areas (Kingett and Choat 1981; Morrison et al. 2008). Manipulative experiments have shown that the use of shelter habitats by juvenile snapper significantly increases in the presence of a predatory threat (Ross et al. 2007).

Snapper are generalist predators which feed on invertebrates from soft sediment and rocky reef habitats (Choat and Kingett 1982; Babcock et al. 1999). They are important predators in structuring shallow reef communities in north-eastern New Zealand, and have been shown to play a significant role in the re-establishment of community-level trophic cascades after the implementation of marine reserves (Shears and Babcock 2002).

Life-history parameters

Snapper display hermaphroditism, with juveniles possessing reproductive tissues of both sexes, with individuals becoming either male or female at sexual maturity. It is estimated that 50 % of the snapper population in Queensland waters are mature at 22 cm FL (~ 25 cm TL) and ~ 2 years of age, and all fish are mature by 33 cm FL and 5 years of age (Ferrell and Sumpton 1997). Recent estimates from NSW waters found that snapper mature at ~ 25 cm FL, although there were latitudinal variations in the size and age at maturity (Stewart et al. 2010). Snapper exhibit sexual dimorphism. Both sexes develop a prominent hump on the forehead as they grow to large sizes, although the hump is more prominent in males than females. Males also develop a bulge on the snout which is not found in females (Moran et al. 1999). Interestingly, these morphological differences do not occur in snapper which inhabit New Zealand waters. Timing of spawning varies regionally in association with day length, food availability and particularly temperature (Scott and Pankhurst 1992; Francis 1994; Henry and Gillanders 1999).

Spawning on parts of the east coast of Australia takes place during winter/spring (Ferrell and Sumpton 1997), with peak spawning probably varying with latitude (Stewart 2008). For example, otolith chemistry profiles of snapper from south-east Australia are consistent with migration of snapper into Port Phillip Bay from coastal areas to spawn during the spring/summer (Hamer et al. 2006). In NSW, peak spawning activity occurs during August (Henry and Gillanders 1999). Spawning appears to occur daily during the late afternoon or early evening (Scott et al. 1993). The average size female (45 cm FL) is estimated to produce around 3.5 million eggs (Ferrell and Sumpton 1997).

Pre-settlement larvae occur in low densities in January and April in subsurface waters on the continental shelf of NSW (Smith 2003). The presence of preflexion larvae over the outer shelf (40 km offshore) during April has been attributed to passive larval advection during coastal upwelling. The lack of postflexion larvae may be explained by the increased ability of larvae to avoid capture, or the movement of larvae to unsampled areas (Smith 2003). Snapper larvae become competent to settle at sizes ≥ 9 mm SL (Trnski 2002). At settlement larvae can cover more than 10 km, at speeds of 10–20 cm s⁻¹, and can exhibit orientated swimming behaviour (Trnski 2002; Clark et al. 2005; Leis et al. 2006). Thus, snapper larvae can often swim faster than ambient currents and can actively swim to settlement sites from continental shelf locations, rather than relying on passive transport via local currents (Clark et al. 2005). Recent evidence also demonstrates that snapper can use olfactory cues to appropriate settlement habitat. In pairwise choice experiments, conducted in New Zealand, larvae swam towards water taken from seagrass beds, rather than water taken from the harbour entrance (Radford et al. 2012).

Development of captive larvae has been well described (Battaglione and Talbot 1992), with larvae hatching at ~ 3 mm TL and feeding commencing after 6 days. Larvae grow at a rate of 0.25–0.28 mm day⁻¹ (Kingsford and Atkinson 1994; Leis et al. 2006). Growth of larvae increased as temperature increased, and larvae reared at 24 °C were 6-fold heavier than larvae reared at 15 °C (Fielder et al. 2005). Metamorphosis is complete by day 25 at ~ 8 to 9 mm TL, and about 22 % of fish in a captive study survived to day 50 or ~ 22 mm FL. The morphology of wild larvae at ages ranging from 0 to 40 days has also been described

(Kingsford and Atkinson 1994). Snapper deposit daily increments in otoliths from the third day post-hatching, with mean estimates of the PLD being 23–27 days (Fowler and Jennings 2003). The PLD for snapper in north-east New Zealand was found to be longer when spawned early in the spawning season when water temperatures were lower, than for snapper spawned later in the season when temperatures were higher, suggesting that metamorphosis is size- rather than age-dependent (Francis et al. 1992a; Francis 1994). Snapper larvae are also known to swim close to the bottom prior to settlement, primarily settling over deep muddy substrates in large bays and estuaries and in sheltered marine waters (Trnski 2002; Hamer and Jenkins 2004; Leis et al. 2006).

Juvenile snapper grow rapidly, attaining ~ 30 cm FL in NSW after ~ 3 years (Ferrell and Sumpton 1997). Rates of growth then slow to 3–4 cm per year at 30 cm TL (Scandol et al. 2008). In New Zealand snapper take 4–5 years to reach 25 cm FL (Willis et al. 2003). Growth of fish in New Zealand is temperature dependent, with growth over a year predicted to change by the equivalent of 8 weeks, if the average annual water temperature changes by 1 °C (Millar et al. 1999). The maximum recorded size of snapper is 1.3 m TL (Gomon et al. 2008) and maximum recorded age in NSW is 40 years (Ferrell and Sumpton 1997), and 60 years old in New Zealand (Henry and Gillanders 1999), with opaque zones in snapper otoliths known to form annually. There is a poor relationship between fish age and length (Ferrell et al. 1992; Francis et al. 1992b).

Post-settlement movement

The fine-scale distribution and movement of juvenile snapper appears to be complex, although at a broad scale they remain in nursery areas for 1–2 years before moving into more open coastal waters (Bell and Worthington 1993; Fowler and Jennings 2003; Wakefield et al. 2011). The patterns of distribution of small juveniles also vary regionally, and in part, are likely to be strongly influenced by the spatial extent of coastal embayment's and estuaries. Such differences indicate that regional studies are required to ensure effective spatial management of snapper populations, particularly spawning and nursery grounds (see Wakefield et al. 2011). No specific spawning or nursery grounds have been identified within the south-east region of Australia, with such areas likely to be more dispersed.

A considerable amount of research on tagging techniques and movement of snapper has been conducted in New Zealand (e.g. Willis and Babcock 1998; Parsons and Egli 2005). Automated ultrasonic tracking of snapper (33–68 cm FL) showed that the species exhibits bimodal patterns of movement (Egli and Babcock 2004). Some fish were resident throughout the ~12 month tracking period, while others were more mobile, leaving the site permanently or returning after periods of up to 83 days. There is some evidence that extreme residency may be promoted by the presence of marine reserves (Parsons et al. 2010). Site fidelity has also been demonstrated in small fish (23 cm FL) over periods >3 years (Willis et al. 2001). Resident snapper have overlapping home ranges <650 m in diameter or 139,600 m² (Parsons et al. 2003). Other tagging studies reveal similar movement with some fish moving <20 km and others moving hundreds of kilometres (Hartill et al. 2003; Moran et al. 2003; Morrison et al. 2008). For example, an intensive tagging study of snapper in Queensland showed that the majority of movements were localised within coastal embayment's (Sumpton et al. 2003). Approximately 1 % of movements exceeded 100 km, with large-scale movements mainly directed northward. Snapper also make onshore–offshore movements in relation to spawning activity (Hamer et al. 2006), and can exhibit diver-positive or neutral behaviour inside marine reserves (Cole 1994).

Population connectivity/stock structure

Snapper populations appear to be 'closed' over relatively small spatial scales (<100 km). This conclusion is supported by multiple studies, using diverse methods in different geographic regions. In Western Australia limited mixing of post-settlement fish among locations within Shark Bay, and between Shark Bay and adjacent ocean waters was indicated using tagging data, and differences in morphometrics and the stable isotopic composition of otolith carbonate among locations (Edmonds et al. 1999; Moran et al. 1999; Bastow et al. 2002; Moran et al. 2003; Norriss et al. 2012). Empirical modelling estimated that 76 % of snapper recruiting to a main oceanic fishing ground near Koks Island (located at the entrance to Shark Bay) would remain within 93 km, even after 6 years (Moran et al. 2003). Genetic differences (allozymes) have also been detected

among snapper from different areas of Shark Bay separated by ~100 km, suggesting that local populations were reproductively isolated (Johnson et al. 1986). Lack of connectivity during the pelagic phase has been partially attributed to local hydrodynamics. Ichthyoplankton data and numerical modelling have shown that eggs and larvae remain within residual eddies corresponding to the four main spawning areas (separated by as little as 10's km), with no mixing among spawning areas observed (Nahas et al. 2003).

Low connectivity among snapper populations has also been found in other geographic regions. Otolith chemistry has been used to demonstrate the importance of local settlement areas for sustaining local snapper fisheries. For example, a significant proportion of sub-adult snapper within Port Phillip Bay (Victoria) and at coastal locations within 200 km west of the bay had originally settled within Port Phillip Bay (Hamer et al. 2005). In South Australia, snapper which occupied a >2,000 km stretch of coastline were shown to represent a single stock, with individuals originating from only one or two nursery areas, and dispersing throughout the different regions between the ages of three to 5 years, before becoming resident (Fowler et al. 2005). In New Zealand genetic differentiation between north-east and southern populations of snapper has been detected using microsatellites, as well as a genetically isolated population within Tasman Bay (Bernal-Ramirez et al. 2003). Genetic patterns were temporally stable over a period of 20 years and were consistent with oceanographic boundaries rather than isolation by distance (Bernal-Ramirez et al. 2003).

There is strong evidence that snapper populations within central NSW are also self-sustaining or relatively 'closed', with significant differences in otolith chemistry of juveniles found among estuaries or groups of estuaries located along the central and southern coast (Gillanders 2002; Gillanders and Kingsford 2003). The nursery areas of adult fish from the fishery in the central region were estimated by examining juvenile portions of adult otoliths, with the vast majority of adult snapper caught in this region originating from local estuaries, 9 % from the far south and ~2 % from other estuaries in NSW (Gillanders 2002). Little is known about levels of pre-settlement connectivity of snapper along the east coast, although modeling of larval trajectories in the region found sites of larval release were most

connected to their adjacent sites (using a PLD of 30 days), with little alongshore spread (Roughan et al. 2011). This scenario is likely to be more complex for species such as snapper, which have the potential to actively influence their dispersal through directed swimming behaviours (discussed under *life-history parameters*). Genetic differentiation and isolation by distance has been detected along the east coast of Australia (central QLD to central NSW) using allozymes, however further analyses using different genetic markers (e.g. microsatellites) are required as variation at allozyme loci may reflect natural selection rather than restricted gene flow (Sumpton et al. 2008).

Red Morwong (*Cheilodactylus fuscus*)

Distribution, abundance, habitat use and diet

Red morwong, *Cheilodactylus fuscus* (family: Cheilodactylidae) are primarily restricted to the south-east coast of Australia, extending from southern Queensland to eastern Victoria, excluding Tasmania, although they have also been recorded in north-eastern New Zealand (Hutchins and Swainston 1986; Gomon et al. 2008). The species is particularly abundant along the southern and central NSW coast where they inhabit rocky reefs to depths of ~30 m, and form local aggregations of three to >100 fish (Kingsford 2001; Lowry and Suthers 2004; Gomon et al. 2008). Within this region, the greatest variation in abundance occurs among reef-habitats and depths rather than at scales of 100's m–10's km alongshore (Curley et al. 2002). These patterns are size-dependent, with large fish (≥ 150 mm SL) generally more abundant in urchin-grazed barrens and sponge dominated habitat than in adjacent *Ecklonia radiata* kelp forest. In contrast, fish <150 mm SL are more abundant in *Ecklonia* habitat and turf algal habitats than in barrens habitat. In northern NSW (<32°S), where urchin barrens habitat is uncommon, red morwong are most abundant on reefs dominated by *Pyura* ascidians (Kingsford 2001). Smaller fish also favour shallower depths (<5 m) on estuarine reefs, particularly during the winter-spring settlement season (Lowry and Suthers 2004). Although red morwong exhibit strong habitat associations during day light hours, fish disperse over a variety of habitats at night (Lowry and Suthers 1998).

Red morwong are benthic carnivores that forage over reef and unconsolidated habitats feeding on a wide variety of prey including amphipods, polychaetes, crabs, molluscs and echinoderms (Bell 1979; Lockett and Suthers 1998). Diet and feeding behaviour are size-specific, with juvenile fish (<200 mm SL) feeding during the day, primarily on amphipods and other small benthic crustaceans. Larger fish feed primarily at night, on brachyurans, molluscs and echinoderms, with ≤ 35 % of their diet being similar to juveniles (Lockett and Suthers 1998).

Life-history parameters

The peak spawning period for red morwong in central NSW occurs during autumn and early winter when they form large spawning aggregations of 80–100 fish at specific locations on exposed coastal reefs (Lowry and Cappel 1999; Lowry and Suthers 2004). Spawning may occur numerous times over the season. Larvae hatch at ~3 mm from small pelagic eggs and remain in surface waters, moving offshore over the continental shelf (Lowry and Cappel 1999). Such offshore transport is consistent with another cheilodactylid common in south-east Australia, the jackass morwong (*Nemadactylus macropterus*), whose larvae have been found up to 250 km offshore in subtropical, subantarctic and intermediate water masses that dominate the region and have a pelagic post-larval phase 'paperfish' stage that settles at around 60–80 mm (Bruce et al. 2001). Red morwong have a similar post-larval stage, with pre-settlement fish ranging from 45 to 90 mm in length (Lowry and Suthers 2004). There are no published studies on the PLD of red morwong, although given the large size at settlement it is likely that they have a long PLD (up to 12 months), similar to that described for jackass morwong. This is supported by the timing of settlement in central NSW where settlement occurs into a variety of shallow reef habitats during winter-spring, approximately 12 months after the main spawning season (Lowry and Suthers 2004). The large size-at-settlement also suggests that active horizontal swimming plays an important role in determining patterns of movement and settlement, consistent with that of jackass morwong (Bruce et al. 2001). Upon settlement, 'paperfish' undergo a rapid metamorphosis from the pelagic post-larval phase into juveniles that are

morphologically similar to adults (Lowry and Cappo 1999).

Juvenile red morwong grow rapidly within the first 12 months post-settlement, reaching a mean size of 146 mm FL after 1 year, and 300 mm TL after 2.5 years (Lowry 2003). The maximum recorded age of red morwong is 40 years (42 cm FL), however fish are thought to be longer-lived as sampled fish were well below the maximum recorded size of 65 cm FL (Lowry 2003; Gomon et al. 2008). While females live longer than males there is no evidence of significant differences in growth rates between sexes (Lowry 2003). Red morwong are estimated to become reproductively mature at 3–5 years of age (Lowry 1997).

Post-settlement movement

Red morwong move from shallow protected waters to deeper and more exposed coastal locations as they increase in size, probably as a consequence of size-related changes in habitat and diet requirements (Lowry and Suthers 2004). Large fish form aggregations in boulder habitat, and with the exception of the mid-summer non-reproductive period, exhibit strong fidelity for their home aggregation (Lowry and Suthers 1998). Movements of 100's m occurs between local aggregations, and the extent and specific location of aggregations varies seasonally, possibly in response to variations in habitat quality, particularly food availability (Lowry and Suthers 1998; Lowry and Cappo 1999). Although the factors which determine the position of aggregations remain unclear, rapid recolonisation (within 2–4 months) by adult fish has been demonstrated after experimental removal of >70 % of adults from aggregations (Lowry and Suthers 2004). Fish >16 cm FL of both sexes occupy diel home ranges of $1,865 \pm 268 \text{ m}^2$ (mean \pm standard error), which approximately doubles during night-time feeding activities ($3,639 \pm 416 \text{ m}^2$) (Lowry and Suthers 1998). Red morwong also demonstrate homing behaviour, travelling 200–900 m and crossing sandy habitat to return to their point of capture (Lockett and Suthers 1998).

Population connectivity/stock structure

There are no studies which investigate population connectivity of red morwong. Connectivity among jackass morwong populations has been well studied in

south-east Australia, with otolith chemistry, larval distribution patterns and oceanography suggesting that jackass morwong populations are regionally self-sustaining despite genetic homogeneity over large spatial scales (Thresher et al. 1994; Bruce et al. 2001; Burridge and Smolenski 2003). These findings provide insight into general mechanisms which could influence connectivity among red morwong populations, and microsatellite markers used for jackass morwong may be of utility in studies of red morwong (Burridge and Smolenski 2000).

Eastern blue groper (*Achoerodus viridis*)

Distribution, abundance, habitat use and diet

Eastern blue groper, *Achoerodus viridis* (family: Labridae) are endemic to southern Australia, occurring from southern Queensland southward to central Victoria, excluding Tasmania (Gomon et al. 2008). Several juveniles were, however, discovered off the northern coast of Tasmania in 2004 (Last et al. 2011). It is most abundant in NSW, with adults inhabiting coastal and estuarine rocky reefs to depths of 60 m (Gomon et al. 2008). In contrast juveniles occur more commonly in estuarine seagrass habitats than rocky reefs (Bell et al. 1987; McNeill et al. 1992; Gillanders and Kingsford 1993). Size-related differences in habitat use are reflected in patterns of abundance and size along an environmental gradient from inside estuaries to the open coast. Numbers of recruits and juvenile fish (<200 mm SL) decrease from inner to outer estuarine sites, whereas large blue groper (>400 mm SL) are found in higher abundances on more exposed coastal reefs (Gillanders 1997b). On coastal reefs, the abundance of large eastern blue groper primarily varies at scales of 100's m rather than kilometres alongshore (Curley et al. 2002). Large blue groper occur in similar abundances in different reef habitats suggesting that they are flexible in their use of habitats (Gillanders and Kingsford 1998; Curley et al. 2002). In contrast, small fish are more numerous in algal dominated habitats such as *Ecklonia* forests (Gillanders and Kingsford 1998). Large blue goppers are most abundant at greater depths than are small and medium-sized fish, which are most abundant in shallow and medium depths, respectively (Gillanders and Kingsford 1993; Gillanders 1997b). Habitat and

depth-related patterns of abundance probably reflect ontogenetic changes in diet requirements and associated foraging behaviour of fish (Gillanders 1995a).

Blue groper are benthic carnivores, with juveniles foraging in shallow fringing habitat, and adults foraging in deeper turf and barrens habitats. Recruits (17–26 mm SL) in seagrass habitats primarily consume tanaid copepods, whereas recruits on rocky reefs primarily eat harpacticoid copepods. Fish on rocky reefs shift their diets to gammarid amphipods and other crustaceans at 50–150 mm SL, and then to mussels and urchins at >300 mm SL (Gillanders 1995a).

Life-history parameters

The reproductive biology of blue groper is comprehensively described in (Gillanders 1995b). They are monandric protogynous hermaphrodites maturing as females at 220–280 mm SL and 2+ to 4+ years of age. Individuals may function as females for 18+ years before transforming into males at 480–580 mm SL; no males <10 years of age have been recorded. The sex ratio of mature fish and whole populations are biased in favour of females. All fish <500 mm SL are females and $\geq 97\%$ of females are brown in colour. In contrast, $\geq 97\%$ of males are blue. Colouration may also be size-dependent as blue females are generally larger than brown females. While the mechanisms which control sex change in blue groper are poorly understood; the timing of sex-change in other species, appears to be an adaptive response to increase reproductive success under specific social-ecological conditions (Munday et al. 2006). Blue groper spawn pelagic eggs over a three-month period in central NSW, starting in June or July (winter) and continuing until October (spring) (Gillanders 1995b). Spawning behaviour has not been observed, however, it is unlikely that fish spawn synchronously as fish with gonads at different stages of development have been recorded concurrently (Gillanders 1999).

The development of blue groper larvae is described by Leis and Hay (2004), with larvae present on the inner continental shelf and individuals 3–8 mm TL relatively abundant during July (winter). Blue groper larvae were relatively abundant in samples taken at 20–30 m, suggesting a strong avoidance of the surface during the day (Leis and Hay 2004). Swimming capabilities of settlement-stage larvae are unknown,

however, blue groper are expected to have some behavioral control over movement from the continental shelf to seagrass beds due to the swimming ability of larvae of species of similar size and state of development (Leis and Hay 2004).

Following their planktonic phase, larvae settle in shallow rocky reefs and estuarine seagrass habitats at around 7–8 mm, and metamorphosis to the juvenile form occurs by ~ 10 mm (Gillanders and Kingsford 1996; Leis and Hay 2004). Manipulative experiments using artificial seagrass units found that blue groper settled in greater numbers to surface habitats that were stationary, compared with those that were moving, or situated at greater depths (Hair et al. 1994). Settlement occurs in distinct seasonal pulses each year, and in central NSW it has been recorded between July and September (McNeill et al. 1992; Worthington et al. 1992), with peak settlement occurring in September–October (Gillanders 1997b). These data in combination with the June–October spawning season and small size at settlement suggest that the pre-settlement phase of blue groper is 2–4 weeks (Gillanders 1995b), although this has not been validated by analyses of larval otoliths.

Growth of recruits in seagrass is relatively slow during winter at 0.21 mm day^{-1} , and then increases, peaking at 0.39 mm day^{-1} immediately prior to fish leaving the habitat (Worthington et al. 1992). The average size of blue groper at 2 years of age is 230 mm SL, 10 years is 480 mm, 20 yrs is 620 mm, and 30 years is 725 mm (Gillanders 1999). Male fish dominate the larger size and age classes, whereas females dominate the smaller size and age classes (Gillanders 1995b). Growth rates are similar for fish inhabiting estuarine reefs and open coastal reefs (Gillanders 1997a). The maximum recorded size of blue groper is 120 cm TL (Kuiter 1996), and maximum estimated age is 35+ years corresponding to <600 mm SL (Gillanders 1995b).

Post-settlement movement

Blue groper which recruit to seagrass grow to ~ 50 mm within 3–4 months before moving to deeper seagrass beds or open reefs (Worthington et al. 1992). The gradual movement of recruits from estuarine habitats to the open coast is supported by patterns of abundance and size structure (described earlier), and otolith chemistry of blue groper sampled along an

environmental gradient from estuarine waters to open coastal reefs (Gillanders and Kingsford 1996; Gillanders 1997b). Scales of movement of large blue groper on coastal reefs have not been quantified, although indirect and anecdotal evidence suggests that fish may be relatively site-attached. Densities of large blue groper (≥ 200 mm SL) are often temporally stable within 1 km stretches of coastal reef in NSW (Curley 2007), and recreational divers often feed recognised individuals at specific sites over long time periods. Furthermore, an acoustic telemetry tagging study of a related species, the western blue groper (*Achoerodus gouldii*), in South Australia indicated that this species is site-attached with mean home-range along-shore length and area estimated at $1,076 \pm 83$ m² (s.e.), and $45,188 \pm 3,497$ m², respectively (n = 11 fish with useful data) (Bryars et al. 2012). Limited movement (<100 m) has also been demonstrated via tagging studies conducted on other temperate labrids including *Pictilabrus laticlavius* and *Notolabrus tetricus*, while others (e.g. *Notolabrus fucicola*) have responded to protection within a 7 km² MPA indicating that at least part of their movements are encompassed by MPA boundaries (Barrett 1995; Edgar and Barrett 1999; Edgar et al. 2004).

Population connectivity/stock structure

Otolith chemistry has been used to demonstrate the importance of estuarine nursery areas for sustaining reef populations of blue groper in central NSW. The concentrations of elements (e.g. Sr, Ba, Mn) in the otoliths of recruits differed between estuarine and rocky reefs. Comparison of the elemental composition of the juvenile section of otoliths from adults collected from coastal reefs showed that 41 % of adults had recruited to estuaries and 59 % had recruited directly to coastal reefs (Gillanders and Kingsford 1996). Otolith chemistry of 165–256 mm SL blue groper in coastal waters of central NSW has also been examined (Dove et al. 1996), and may be of use for interpreting results of future studies.

Discussion

Knowledge of the biology and ecology of the reviewed fishes in south-east Australia is generally limited to basic patterns of abundance, habitat use, age and

growth (Table 1). A few species are well studied with respect to select life-history parameters, such as growth (eastern blue groper, luderick, yellowfin bream, tarwhine, snapper), post-settlement movement (red morwong), and larval ecology (yellowfin bream). In contrast, knowledge of the overall biology of rock blackfish is largely based on a few scientific studies and anecdotal information. Importantly, empirical data on levels of pre- and post-settlement connectivity are rudimentary for most species, despite the fact that it is often identified as a critical data gap for effective spatial management (Palumbi 2004; Sale et al. 2005; Kaplan et al. 2010; Grüss et al. 2011). In the case of MPAs, these factors will influence potential increases in density, mean size/age, and biomass of exploited species within MPA boundaries; and in turn the net export of post-settlement fishes and propagules to unprotected areas (Gerber et al. 2002). Significant progress has been made in understanding these processes with respect to MPA networks in other geographic areas (e.g. The Great Barrier Reef, Papua New Guinea, Mediterranean), and provide useful templates for future research in south-east Australia (e.g. Planes et al. 2009; Di Franco et al. 2012; Harrison Hugo et al. 2012).

Given the challenges of empirically determining connectivity patterns, estimates derived from biophysical transport modelling provide the capacity to predict with reasonable levels of precision connectivity across multiple spatial and temporal scales (Cowen et al. 2007). These models have the ability to provide estimates of relative levels of potential larval exchange among all sections of habitat within a domain (e.g. James et al. 2002; Paris and Cowen 2004). The south-east Australia region is characterised by highly complex oceanography on the continental shelf and offshore waters, with flow dominated by the southward flowing, warm East Australian Current (EAC), northward flowing counter current, and periods of strong upwelling (Middleton et al. 1996; Suthers et al. 2011). At a large scale, the EAC and its eddy field strongly influence the patterns of pre-settlement movement of marine species in the region (Roughan et al. 2011). There are generalised (or mean) patterns of larval dispersal in the region dependant on the latitude and distance offshore of larval release, and length of the PLD (Roughan et al. 2011). Improvements in biophysical modelling approaches will require good information on early-life history,

Table 1 Status of biological knowledge for key harvested coastal fishes from south-east Australia

		Red morwong (<i>C. fuscus</i>)	Eastern blue groper (<i>A. viridis</i>)	Eastern rock Blackfish (<i>G. elevata</i>)	Luderick (<i>G. tricuspidata</i>)	Yellowfin bream (<i>A. australis</i>)	Tarwhine (<i>R. sarba</i>)	Snapper (<i>P. auratus</i>)
Spatial abundance patterns	- recruits	Light grey	Light grey	Light grey	Dark grey	Dark grey	Dark grey	Dark grey
	- juveniles	Dark grey	Dark grey	Light grey	Dark grey	Dark grey	Dark grey	Dark grey
	- adults	Dark grey	Dark grey	Light grey	Dark grey	Dark grey	Light grey	Dark grey
Temporal abundance patterns	- recruits	Light grey	Dark grey	Light grey	Dark grey	Dark grey	Dark grey	Light grey
	- juveniles	Light grey	Dark grey	Light grey	Dark grey	Dark grey	Dark grey	Light grey
	- adults	Light grey	Dark grey	Light grey	Dark grey	Light grey	Light grey	Light grey
Habitat/depth preference	- recruits	Light grey	Dark grey	Light grey	Dark grey	Dark grey	Dark grey	Dark grey
	- juveniles	Light grey	Dark grey	Light grey	Dark grey	Dark grey	Dark grey	Dark grey
	- adults	Light grey	Dark grey	Light grey	Dark grey	Light grey	Light grey	Light grey
Growth rates		Light grey	Dark grey	Light grey	Dark grey	Dark grey	Dark grey	Dark grey
Age to maturity		Light grey	Dark grey	Light grey	Dark grey	Dark grey	Dark grey	Dark grey
Spawning	- time/duration	Light grey	Light grey	Light grey	Light grey	Light grey	Light grey	Light grey
	- location	Light grey	Light grey	Light grey	Light grey	Light grey	Light grey	Light grey
Max age/size		Light grey	Dark grey	Light grey	Dark grey	Light grey	Dark grey	Dark grey
Reproductive output		Light grey	Dark grey	Light grey	Dark grey	Dark grey	Dark grey	Dark grey
Pre-settlement	- duration	Light grey	Light grey	Light grey	Dark grey	Dark grey	Dark grey	Dark grey
	- behaviour	Light grey	Light grey	Light grey	Dark grey	Dark grey	Dark grey	Dark grey
	- connectivity	Light grey	Light grey	Light grey	Dark grey	Dark grey	Dark grey	Dark grey
Post-settlement movement	- movement	Dark grey	Light grey	Light grey	Dark grey	Light grey	Light grey	Light grey
	- connectivity	Light grey	Light grey	Light grey	Dark grey	Light grey	Light grey	Light grey
Population genetic structure		Light grey	Light grey	Light grey	Dark grey	Dark grey	Light grey	Light grey

Categorisation is qualitative. *Dark grey* good knowledge/well published and studied. *Light grey* limited published information/further study required. *White* no published information/anecdotal information only

including: PLD, the ability of larvae to swim or vertically migrate and other pre-settlement behaviours (e.g. sensory abilities), and settlement habitat preferences. Although larval behaviour, timing of reproduction, and settlement habitats have been examined for several of the reviewed species (e.g. snapper, yellowfin bream, blue groper, luderick), PLDs have rarely been validated using otolith analyses, and there are few empirical data on temporally consistent locations for spawning aggregations for any species. An exception to this is snapper where PLD estimates are available from other regions. For this reason, snapper would be an ideal candidate for initial research, particularly as the understanding of factors affecting pre-settlement dispersal of snapper in other areas of its distribution is comparatively advanced (e.g. Western and Southern Australia, New Zealand).

Knowledge of post-settlement movement of the species examined is based largely on traditional

tagging techniques (e.g. dart, T-bar tags) deployed in specific geographic regions. There is no published information on real time movements, relative habitat use, effective home ranges, and potential barriers to movement for the reviewed species in south-east Australia (but see red morwong). More precise data on movement will limit biases associated with the use of over-simplified movement patterns in the evaluation of MPA effectiveness (Grüss et al. 2011). For example, evidence of bi-modal movement strategies has been documented for yellowfin bream, luderick, and snapper, with some individuals being relatively sedentary (moving < km's) and others being highly mobile (moving 10's–100's km). In such cases, relatively small MPAs could be used to protect a portion of the population. The application of alternative methods including acoustic tracking and telemetry (real-time movements) and otolith chemistry will be required to address these gaps. Considerable advances have been

made in the application of these tools in recent years (Parsons et al. 2010; Bryars et al. 2012; Di Franco et al. 2012; Sturrock et al. 2012), and more extensive use of them could be made in south-east Australia.

A crucial data gap relating to post-settlement connectivity is to identify the relative contributions of different estuaries for maintaining adult stocks. Five of the reviewed species (groper, luderick, bream, tarwhine and snapper) primarily use estuarine habitats as nurseries, before becoming more widely distributed throughout estuarine and coastal waters as juveniles and adults. Existing studies using otolith chemistry to examine estuarine-coast connectivity are limited to groper and snapper, but indicate that there is likely to be sufficient environmental variability within estuaries, among estuaries, between open coastal environments, and among coastal reefs in NSW to facilitate the use of otolith chemistry for determining population connectivity of a variety of fishes across a range of spatial scales (e.g. Gillanders 2002; Curley 2007). Otolith chemistry is particularly advantageous as this technique overcomes fundamental disadvantages associated with conventional tagging techniques, such as the need to tag a large number of individuals in order to get meaningful sample sizes, difficulties in tagging juveniles and adults, high rates of mortality in early life history, and sub-lethal effects which may confound estimates of movement (Gillanders 2002). Furthermore, otolith chemistry can give insight into population connectivity when levels of mixing prevent genetic differentiation (Thorrold et al. 2001; Rooker et al. 2003), which is likely for many species in NSW.

Limited data on population genetics of luderick and yellowfin bream are available for south-east Australia. It has been hypothesised that lack of detectable genetic differentiation within these and other fishes (e.g. white-ear damselfish, *Parma microlepis*) and invertebrates in this region is a consequence of large effective population sizes, relatively continuous habitats, and sufficient levels of gene flow due to EAC driven transport of larvae (Curley and Gillings 2009). However, genetic homogeneity should not be assumed without empirical evidence. Population genetic structure may be detectable between estuarine and coastal populations (e.g. snapper in Western Australia), or with finer-scale genetic sampling (e.g. parentage analyses; Harrison Hugo et al. 2012). Information on population genetics of the reviewed species will also provide a valuable baseline with which to assess

potential changes. For example, population declines have been associated with loss of genetic diversity which may reduce adaptability, population persistence and productivity (Hauser et al. 2002).

Recent advances in methodologies such as acoustic tracking, otolith microchemistry, hydrodynamic models and population genetics are now providing an increased capacity to examine population connectivity at higher spatial and temporal resolutions than ever before (Kaplan et al. 2010). These developments have been accompanied by a significant increase in the availability of fine-scale data on the spatial distribution of marine habitats which will allow species-habitat associations to be examined in greater detail (Bax and Williams 2001; Creese et al. 2009; Jordan et al. 2010). The incorporation of high resolution spatial data on both movement and habitat extent and distribution will provide an increasingly powerful tool to quantify aspects of the life history and ecology of coastal species in order to evaluate the spatial arrangement of MPAs required for their effective conservation. Linking fine-scale hydrodynamic models and maps of seabed habitats will also considerably increase the precision of models estimating patterns of larval sources and sinks, and allow such evaluations at the scale of the majority of MPA zones in south-east Australia. The broad principles of MPA design in order to maximise connectivity for coral reefs systems with limited scientific information are detailed in McCook et al. (2009), and these are just as applicable to subtropical and temperate ecosystems in many regions worldwide.

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