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Larval dispersal and movement patterns of coral reef fishes, and implications for marine reserve network design

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ABSTRACT

Well-designed and effectively managed networks of marine reserves can be effective tools for both fisheries management and biodiversity conservation. Connectivity, the demographic linking of local populations through the dispersal of individuals as larvae, juveniles or adults, is a key ecological factor to consider in marine reserve design, since it has important implications for the persistence of metapopulations and their recovery from disturbance. For marine reserves to protect biodiversity and enhance populations of species in fished areas, they must be able to sustain focal species (particularly fishery species) within their boundaries, and be spaced such that they can function as mutually replenishing networks whilst providing recruitment subsidies to fished areas. Thus the configuration (size, spacing and location) of individual reserves within a network should be informed by larval dispersal and movement patterns of the species for which protection is required. In the past, empirical data regarding larval dispersal and movement patterns of adults and juveniles of many tropical marine species have been unavailable or inaccessible to practitioners responsible for marine reserve design. Recent empirical studies using new technologies have also provided fresh insights into movement patterns of many species and redefined our understanding of connectivity among populations through larval dispersal. Our review of movement patterns of 34 families (210 species) of coral reef fishes demonstrates that movement patterns (home ranges, ontogenetic shifts and spawning migrations) vary among and within species, and are influenced by a range of factors (e.g. size, sex, behaviour, density, habitat characteristics, season, tide and time of day). Some species move <0.1–0.5 km (e.g. damselfishes, butterflyfishes and angelfishes), <0.5–3 km (e.g. most parrotfishes, goatfishes and surgeonfishes) or 3–10 km (e.g. large parrotfishes and wrasses), while others move tens to hundreds (e.g. some groupers, emperors, snappers and jacks) or thousands of kilometres (e.g. some sharks and tuna). Larval dispersal distances tend to be <5–15 km, and self-recruitment is common. Synthesising this information allows us, for the first time, to provide species, specific advice on the size, spacing and location of marine reserves in tropical marine ecosystems to maximise benefits for conservation and fisheries management for a range of taxa. We recommend that: (*i*) marine reserves should be more than twice the size of the home range of focal species (in all directions), thus marine reserves of various sizes will be required depending on which species require protection, how far they move, and if other effective protection is in place outside reserves; (*ii*) reserve spacing should be <15 km, with smaller reserves spaced more closely; and (*iii*) marine

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reserves should include habitats that are critical to the life history of focal species (e.g. home ranges, nursery grounds, migration corridors and spawning aggregations), and be located to accommodate movement patterns among these. We also provide practical advice for practitioners on how to use this information to design, evaluate and monitor the effectiveness of marine reserve networks within broader ecological, socioeconomic and management contexts.

Key words: connectivity, larval, dispersal, movement, marine, reserve, tropical.

CONTENTS

I. INTRODUCTION

Marine reserves (defined here as areas of ocean that are protected from extractive and destructive activities) can be an effective tool for both conservation and fisheries management in tropical marine ecosystems (Russ, 2002; Lester *et al.*, 2009). Marine reserves can increase the diversity, density, biomass, body size and reproductive potential of coral reef fishes (particularly focal fisheries species) within their boundaries (Lester *et al.*, 2009; Babcock *et al.*, 2010; Russ & Alcala, 2011), and provide conservation and fisheries benefits to surrounding areas through the export of eggs, larvae, juveniles and adults to other reserves and fished areas (Russ, 2002; Halpern, Lester & Kellner, 2010; Harrison *et al.*, 2012).

The design and effective implementation of networks of marine reserves is critical to maximise their benefits to both conservation and fisheries management (Walmsley & White, 2003; Gaines *et al.*, 2010). Connectivity, the demographic linking of local populations through the dispersal of individuals as larvae, juveniles or adults (Sale *et al.*, 2005), is a key ecological factor to consider in marine reserve design, since it has important implications for the persistence of metapopulations and their recovery from disturbance (Botsford, Micheli & Hastings, 2003; Almany *et al.*, 2009; McCook *et al.*, 2009). Of particular importance are ecological patterns of connectivity through larval transport and juvenile or adult movement, which operate at different temporal and spatial scales than those that influence genetic (or evolutionary) patterns of connectivity (Cowen, Paris & Srinivasan, 2006; Foster *et al.*, 2012).

Most coral reef fish species have a bipartite life cycle where larvae are pelagic before settling out of the plankton and forming an association with coral reefs. These species vary greatly in how far they move during their life-history phases (Palumbi, 2004), although larvae of most species have the potential to move much longer distances (tens to hundreds of kilometres: Cowen *et al.*, 2006; Jones *et al.*, 2009) than adults and juveniles, which tend to be more sedentary (with home ranges <1 m to a few kilometres: Russ, 2002). Exceptions include coral reef species where adults and juveniles exhibit large-scale (tens to hundreds of kilometres) ontogenetic shifts in habitat use (e.g. among coral reef, mangrove and seagrass habitats: Nagelkerken *et al.*, 2001; Chin *et al.*, 2013*a*) or migrations to fish spawning aggregation sites (e.g. Starr *et al.*, 2007; Rhodes *et al.*, 2012), and pelagic species that range over much longer distances (hundreds to thousands of kilometres e.g. Ortiz *et al.*, 2003).

When adults and juveniles leave the boundary of a marine reserve, they become vulnerable to fishing mortality (Kramer & Chapman, 1999; Gaines *et al.*, 2010). However, larvae leaving a reserve can generally disperse without elevated risk because of their small size and limited exposure to fisheries (Gaines *et al.*, 2010). Thus, consideration of the spatial scale of movement of coral reef fish species at each stage in their life cycle is critically important in designing the configuration (size, spacing and location) of networks of tropical marine reserves (Kramer & Chapman, 1999; Palumbi, 2004; Botsford *et al.*, 2009*b*; Gaines *et al.*, 2010).

Where movement patterns of focal species are known, this information can be used to inform guidelines or decisions about the configuration of marine reserves to maximise benefits to both fisheries and conservation (Botsford *et al.*, 2003; Palumbi, 2004; Jones, Srinivasan & Almany, 2007; Gaines *et al.*, 2010). For example, movement studies were used to develop rules of thumb for minimum and preferred size ranges of marine protected areas (MPAs) in a temperate system in California, and species-specific information was used to communicate with stakeholders regarding which types of species would best be protected by MPAs of different sizes (Gleason *et al.*, 2013; Saarman *et al.*, 2013). However, the empirical information required to apply this approach to tropical marine ecosystems has yet to be synthesised in a format useful for marine reserve design (Sale *et al.*, 2005; Botsford *et al.*, 2009*b*). Recent advances in technology, such as the use of acoustic and satellite telemetry, have also provided new insights into spatiotemporal movements and habitat requirements of adults and juveniles of many species that need to be considered.

Recent empirical studies have also redefined our understanding of larval dispersal and connectivity among populations (Jones *et al.*, 2009; Harrison *et al.*, 2012; Almany *et al.*, 2013) These studies have demonstrated that self-recruitment (the proportion of recruits that are the offspring of parents in the same population) and restricted larval dispersal are more common than previously thought, indicating that even small marine reserves can provide recruitment benefits within and close to their boundaries (Planes, Jones & Thorrold, 2009; Weeks *et al.*, 2010). These results provide an imperative to update recommendations for marine reserve network design, and to re-examine the level of benefits that many small and closely spaced reserves can generate for fish populations, particularly if they are combined with other management tools (Hilborn, Micheli & De Leo, 2006).

Here we review and synthesise the best available information regarding adult, juvenile and larval movement patterns of coral reef and associated (coastal pelagic) fish species, much of which has only become available since the most recent reviews on movement and larval dispersal of these species were conducted by Kramer & Chapman (1999) and Jones *et al.* (2009). We use this information to refine advice regarding the configuration of networks of marine reserves, and implications for other management strategies, to achieve conservation and fisheries objectives in tropical marine ecosystems. We also provide practical advice for field practitioners regarding how to use this information to improve marine reserve network design within broader ecological and socioeconomic contexts.

II. MOVEMENT PATTERNS OF ADULTS AND JUVENILES

We distinguish three types of movement of adult and juvenile coral reef and coastal pelagic fish species: home ranges, spawning migrations and ontogenetic shifts in habitat. Each of these movement types is described below, based on a synthesis of the best available information for 34 families and 210 species provided in Table 1 (for additional details see online Appendix S1).

This information is extremely useful for MPA practitioners, since it will allow them to undertake detailed discussions with governments, fishermen, communities and other stakeholders regarding movement patterns of focal species for protection and the implications of these for marine reserve size. To facilitate such discussions, we provide an illustrative figure that summarises fish movement for a range of taxa by distance (Fig. 1). In this figure, we used conservative measurements of how far fish move that excluded outliers and were indicative of movement patterns for taxa across studies.

In most cases, we used empirical studies that directly measured movement using methods that include tag-mark-recapture, passive and active acoustic telemetry, satellite tracking and underwater observations (see online Appendix S1). Only in rare cases, where direct empirical measurements were either not available or inadequately represented movement patterns of key species, did we include estimates derived from other methods, i.e. we used size-class distributions and age estimations from otoliths to describe ontogenetic habitat shifts by a focal fisheries species (*Caranx sexfasciatus*: Maypa, 2012), and estimates of spawning movements of an endangered wrasse (*Cheilinus undulatus*) and several species of herbivore from a recognised expert in that field (Colin, 2010, 2012). These estimates may require validation by empirical measurements of movement in future.

Each of the methods used to measure movement patterns of adults and juveniles has its strengths and weaknesses. For well-designed experiments (with adequate sample sizes conducted over appropriate spatiotemporal scales for the study species), methods that directly measure both the spatial and temporal components of movement patterns are considered the most reliable (for further details see online Appendix S2).

For acoustic telemetry, spatial data is typically analysed and subsequently viewed using several measurements (see online Appendix S2). Where possible, we reported kernel utilisation distributions with a 95% probability of location (KUD95), because they provide a conservative estimate of home range that includes both the core area of use and migrations to feeding and often to spawning areas. Where KUD95 was not available, we used the minimum convex polygon (MCP), which provides a more simplistic estimation of the home range of the individuals examined during the study.

Because empirical measurements of movement were provided in the literature as both linear distances and home ranges (area), we standardised by converting all

Table 1. Summary of movement patterns of adult and juvenile coral reef and coastal pelagic fishes, and recommended minimum marine reserve size (more than twice the home range or core area of use of focal species in all directions, where applicable). More detailed information for each species and study is provided as Appendix S1.

CLASS Family (common name)	Recommended minimum marine reserve size (linear distance in km)	Movement (linear distance in km) Home range and territories	Spawning (breeding) migrations	Ontogenetic habitat shifts	Other long-term movements (core areas of use)	Sources
OSTEICHTHYES						
Acanthuridae (surgeonfishes and unicornfishes)						
Acanthurus leucosternon and *Naso vlamingii*	0.2	<0.1	—	—	—	Robertson, Polunin & Leighton (1979); Abesamis & Russ (2005)
Acanthurus chirugus, *A. coeruleus* and *Ctenochaetus striatus*	0.6	<0.3	—	—	—	Bell & Kramer (2000); Chapman & Kramer (2000); Krone *et al.* (2008); Garcia *et al.* (2011); Claydon, McCormick & Jones (2012); Colin (2012)
Acanthurus lineatus, *Naso unicornis*, *Zebrasoma flavescens* and *Z. scopas*	2	<1	—	—	—	Robertson *et al.* (1979); Craig (1996); Craig *et al.* (1997); Meyer & Holland (2005); Hardman *et al.* (2010); Claisse *et al.* (2011); Marshell *et al.* (2011)
Acanthurus bahianus, *A. blochii* and *A. nigrofuscus*	6	<3	—	—	—	Mazeroll & Montgomery (1995); Chapman & Kramer (2000); Munro (2000); Meyer *et al.* (2010*a*); Colin (2012)
Naso hexacanthus and *N. lituratus*	10	<5	—	—	—	Meyer *et al.* (2010*a*); Marshell *et al.* (2011)
Abulidae (bonefishes)						
Albula vulpes	—	—	—	—	<10	Dunlop & Mann (2012)
Anguillidae (freshwater eels)						
Anguilla bicolor bicolor	—	—	—	<10	—	Chino & Arai (2010)
Apogonidae (cardinalfishes)						
Apogon doederlini, *Cheilodipterus artus* and *C. quinquilineatus*	<0.1	<0.01	—	—	—	Marnane (2000)
Balistidae (triggerfishes)						
Balistes capriscus	—	—	—	—	<20	Addis, Patterson & Dance (2007)
Carangidae (jacks)						
Caranx ferdau, *C. fulvoguttatus*, *C. orthogrammus*, *C. papuensis* and *C. ruber*	10	<5	—	—	—	Chapman & Kramer (2000); Tagawa & Tam (2006); Pillans *et al.* (2011); Dunlop & Mann (2012)
Caranx ignobilis	20	—	—	<5	<20–300 (<5)	Smith & Parrish (2002); Wetherbee *et al.* (2004); Lowe, Wetherbee & Meyer (2006); Tagawa & Tam (2006); Meyer *et al.* (2007*a*); Dunlop & Mann (2012)

Table 1. Continued

CLASS Family (common name)	Recommended minimum marine reserve size (linear distance in km)	Movement (linear distance in km) Home range and territories	Spawning (breeding) migrations	Ontogenetic habitat shifts	Other long-term movements (core areas of use)	Sources
Caranx melampygus	20	—	—	—	<100 (<10)	Holland *et al.* (1996); Meyer & Honebrink (2005); Tagawa & Tam (2006); Dunlop & Mann (2012)
Caranx sexfasciatus	6	—	—	<3	<200 (<3)	Tagawa & Tam (2006); Dunlop & Mann (2012); Maypa (2012)
Pseudocaranx dentex	20	—	—	—	<50 (<10)	Afonso *et al.* (2009)
Scomberoides commersonianus	2	—	—	—	<10 (<1)	Dunlop & Mann (2012)
Seriola dumerili, *S. lanlandi* and *S. riviolana*	10	—	—	—	<3000 (<5)	Gillanders, Ferrell & Andrew (2001); Tagawa & Tam (2006); Hutson *et al.* (2007)
Chaetodontidae (butterflyfishes)						
Chelmon rostratus, *Chaetodon kleini*, *C. multicinctus*, *C. ornatissimus*, *C. plebius*, *C. quadrimaculatus*, *C. rainfordi*, *C. trifasciatus* and *C. unimaculatus*	0.2	<0.1	—	—	—	Hourigan (1987); Fowler (1988)
Chaetodon striatus	0.6	<0.3	—	—	—	Chapman & Kramer (2000)
Chaetodon auriga	1	<0.5	—	—	—	Hourigan (1987)
Coryphaenidae (dolphinfishes)						
Coryphaena hippurus	—	—	—	—	<70	Dunlop & Mann (2012)
Epinephelidae (groupers)						
Cephalopholis argus, *C. cruenata*, *C. cyanostigma*, *C. hemistiktos*, *C.minatus*, *Ephinephelus adscensions* and *E. fulvus*	0.2	<0.1	—	—	—	Shpigel & Fishelson (1991); Chapman & Kramer (2000); Beets *et al.* (2003); Popple & Hunte (2005); Zeller, Stoute & Russ (2003)
Epinephelus marginatus, *E. multinotatus*, *E. tauvina* and *Variola louti*	6	<3	—	—	—	Afonso, Fontes & Santos (2011); Pillans *et al.* (2011)
Cephalopholis sonnerati, *Epinephelus coicoides* and *E. maculatus*	10	<5	—	—	—	Sawynok (2004); Chateau & Wantiez (2008*b*); Dunlop & Mann (2012)
E. malabaricus	20	—	—	—	<10	Dunlop & Mann (2012)
E. tukula	6	—	—	—	<20 (<3)	Dunlop & Mann (2012)
E. morio	—	—	—	—	<800	Beaumariage (1969); Moe (1966)

Table 1. Continued

CLASS		Movement (linear distance in km)				
Family (common name)	Recommended minimum marine reserve size (linear distance in km)	Home range and territories	Spawning (breeding) migrations	Ontogenetic habitat shifts	Other long-term movements (core areas of use)	Sources
E. guttatus	1	0.3	<30	—	—	Burnett-Herkes (1975); Sadovy, Rosario & Roman (1994); Shapiro, Garcia-Moliner & Sadovy (1994); Luckhurst (1998); Jimenez & Fernandez (2001); Beets *et al.* (2003); Nemeth (2005); Nemeth *et al.* (2007)
E. fuscoguttatus	—	—	<30	—	—	Rhodes *et al.* (2012)
E. polyphekadion	—	—	<40	—	—	(K. Rhodes & Y. Sadovy de Mitcheson, unpublished data)
E. striatus	—	—	<300	—	—	Colin (1992); Carter, Marrow & Pryor (1994); Bolden (2000); Starr *et al.* (2007)
Mycteroperca microlepis	2	<1	—	—	<300 (<20)	Moe (1966); Beaumariage (1969); Kiel (2004); McGovern *et al.* (2005); Addis *et al.* (2007); Biesinger *et al.* (2013)
Plectropomus areolatus	2	<1	<30	—	—	Tupper (2007); Rhodes & Tupper (2008); Hutchinson & Rhodes (2010); Wilson, Rhodes & Rotinsulu (2010); (G. Almany & K. Rhodes *et al.*, unpublished data)
Plectropomus leopardus	6	<3	<10	—	—	Samoilys (1997); Zeller (1997, 1998); Zeller & Russ (1998); Zeller *et al.* (2003); Chateau & Wantiez (2008*b*); Pillans *et al.* (2011)
Serranus cabrilla	4	<2	—	—	—	Alós *et al.* (2011)
Gobiidae (gobies)						
Amblygobius bynoensis, *A. phalaena*, *Asterropteryx semipunctatus*, *Istigobius goldmanni* and *Valencienna muralis*	<0.1	<0.01	—	—	—	Hernaman (2003)
Haemulidae (grunts and sweetlips)						
Haemulon carbonarium and *H. chrysargyreum*	0.2	<0.1	—	—	—	Chapman & Kramer (2000)
H. sciurus	2	<1	—	—	—	Burke (1995); Beets *et al.* (2003); Verweij & Nagelkerken (2007)
H. plumieri	2	<1	—	—	<10	Moe (1966); Ogden & Ehrlich (1977); Tulevech (1991) in Burke (1995); Tulevech & Recksiek (1994)
H. flavolineatum	1	<0.5	—	<3	—	Ogden & Ehrlich (1977); Burke (1995); Chapman & Kramer (2000); Verweij & Nagelkerken (2007)

Table 1. Continued

CLASS Family (common name)	Recommended minimum marine reserve size (linear distance in km)	Movement (linear distance in km) Home range and territories	Spawning (breeding) migrations	Ontogenetic habitat shifts	Other long-term movements (core areas of use)	Sources
Plectorhinchus flavomaculatus	6	—	—	—	<200 (<3)	Kaunda-Arara & Rose (2004); Dunlop & Mann (2012)
Pomadasys furcatum	6	—	—	—	<20 (<3)	Dunlop & Mann (2012)
Pomadasys kaakan	20	—	—	—	<70 (<10)	Dunlop & Mann (2012)
Holocentridae (soldierfishes and squirrelfishes)						
Holocentrus adscensionis, *H. rufus* and *Myripristis jacobus*	0.2	<0.1	—	—	—	Chapman & Kramer (2000)
Istiophoridae (billfishes)						
Istiophorus platypterus	—	—	—	—	<4000	Hoolihan (2003); Ortiz *et al.* (2003); Dunlop & Mann (2012)
Makaira indica and *Makaira nigricanus*	—	—	—	—	<15000	Gunn, Patterson & Pepperell (2003); Ortiz *et al.* (2003); Dunlop & Mann (2012)
Kyphosidae (drummers)						
Kyphosus sectatrix	6	<3	—	—	—	Chapman & Kramer (2000); Eristhee & Oxenford (2001)
Kyphosus sedneyanus	10	<5	—	—	—	Pillans *et al.* (2011)
Labridae (wrasses)						
Bodianus rufus, *Halichoeres garnoti* and *Thalassoma bifasciatum*	0.2	<0.1	—	—	—	Chapman & Kramer (2000); Overholtzer-McLeod (2005)
Coris aygula	10	<5	—	—	—	Pillans *et al.* (2011)
Cheilinus undulatus	20	<10	—	—	—	Tupper (2007); Chateau & Wantiez (2007); Colin (2010, 2012)
Lethrinidae (emperors)						
Lethrinus nebulosus	10	<5	—	—	—	Kaunda-Arara & Rose (2004); Chateau & Wantiez (2008*a*); Pillans *et al.* (2011)
Lethrinus mahsena	10	—	—	—	<200 (<5)	Kaunda-Arara & Rose (2004)
Lethrinus miniatus	10	—	—	—	<200 (<5)	Kaunda-Arara & Rose (2004): (B. Sawynok, unpublished data) in Williams *et al.* (2010)
Lutjanidae (snappers)						
Lutjanus carponotatus, *L. fulviflamma* and *Ocyurus chrysurus*	0.2	<0.1	—	—	—	Zeller *et al.* (2003); Dorenbosch *et al.* (2004); Watson, Munro & Gell (2002)
L. ehrenbergii	0.2	<0.1	—	—	>30	McMahon *et al.* (2012); Dorenbosch *et al.* (2004)
Lutjanus russelli	2	<1	—	—	—	Dunlop & Mann (2012)
Lutjanus apodus	2	<1	—	<0.3	—	Chapman & Kramer (2000); Munro (2000); Verweij *et al.* (2007)

Table 1. Continued

CLASS		Movement (linear distance in km)				
Family (common name)	Recommended minimum marine reserve size (linear distance in km)	Home range and territories	Spawning (breeding) migrations	Ontogenetic habitat shifts	Other long-term movements (core areas of use)	Sources
Lutjanus griseus	2	<1	—	—	<20	Lou *et al.* (2009)
Lutjanus johni	6	<3	—	—	—	Sawynok (2004)
Lutjanus aya and *L. rivulatus*	6	—	—	—	<200 (<3)	Moe (1966); Dunlop & Mann (2012)
Lutjanus argentimaculatus	6	—	—	—	<400 (<3)	Sawynok (2004); Dunlop & Mann (2012)
Lutjanus campechanus	10	<1	—	—	<400 (<5)	Beaumariage (1969); Fable (1980); Szedlmayer & Shipp (1994); Szedlmayer (1997); Patterson *et al.* (2001); Addis *et al.* (2007)
Aprion virescens	20	<10	—	—	<20	Meyer, Papastamatiou & Holland (2007)
Monacanthidae (filefishes)						
Cantherhines pullus	0.2	<0.1	—	—	—	Chapman & Kramer (2000)
Mullidae (goatfishes)						
Mulloidichthys martinicus and *Parupeneus porhyreus*	1	<0.5	—	—	—	Chapman & Kramer (2000); Meyer *et al.* (2000)
Mulloidichthys flavolineatus, *Parupeneus cyclostomus* and *P. trifasciatus*	2	<1	—	—	—	Holland *et al.* (1993*a*); Meyer *et al.* (2010*a*)
Muraenidae (moray eels)						
Gymnothorax prasinus and *G. moringa*	0.2	<0.1	—	—	—	Chapman & Kramer (2000); Bassett & Montgomery (2011)
Pomacanthidae (angelfishes)						
Centropyge ferrugatus	<0.1	<0.01	—	—	—	Sakai & Kohda (1995)
Holocanthus tricolor, *Pomacanthus paru* and *P. arcuatus*	0.6	<0.3	—	—	—	Hourigan *et al.* (1989); Chapman & Kramer (2000)
Pomacentridae (damselfishes)						
Dascyllus albisella, *D. aruanus*, *Dischistodus perspicillatus*, *D. prosopotaenia*, *Hemiglyphidodon plagiometapon*, *Neoglyphidodon nigroris*, *Plectroglyphidodon lacrymatus*,	<0.1	<0.02	—	—	—	Bartels (1984); Booth (1991); Frederick (1997); Forrester (1990); Green (1994); Holbrook, Forrester & Schmitt (2000); Ceccarelli (2007)

Table 1. Continued

CLASS		Movement (linear distance in km)				
Family (common name)	Recommended minimum marine reserve size (linear distance in km)	Home range and territories	Spawning (breeding) migrations	Ontogenetic habitat shifts	Other long-term movements (core areas of use)	Sources
Pomacentrus adelus, *P. bankanensis*, *P. burroughi*, *P. chrysurus*, *P. tripunctactus*, *P. wardi*, *Stegastes adjusta* and *S. apicalis*						
Chromis fumea and *Microspathodon chrysurus*	0.2	<0.07	—	—	—	Chapman & Kramer (2000); Wantiez & Thollot (2000)
Abudefduf saxatalis	0.4	<0.2	—	—	—	Chapman & Kramer (2000)
Scaridae (parrotfishes)						
Scarus iserti and *S. vetula*, *Sparisoma chyrsopterum*	0.2	<0.1	—	—	<30	Chapman & Kramer (2000); Munro (2000); Mumby & Wabnitz (2002)
Sparisoma aurofrenatum, *S. rubripinne* and *S. viride*, *Chlorurus sordidus*	1	<0.5	—	—	<20 (<3)	Dubin (1981*b*); Clavijo (1982) & Munoz (1996) in Mumby & Wabnitz (2002); Colin (2012); van Rooij, Kroon & Videler (1996); Overholtzer & Motta (1999); Chapman & Kramer (2000); Munro (2000); Mumby & Wabnitz (2002); Garcia *et al.* (2011)
Scarus coeruleus, *S. taeniopterus* and *S. rivulatus*	2	<1	—	—	—	Dubin (1981*a*); Overholtzer & Motta (1999); Lindholm *et al.* (2006); Fox (2012); Welsh & Bellwood (2012)
Chlorurus frontalis, *C. microrhinos*, *C. perspicillatus*, *C. sordidus*, *Scarus prasiognathus* and *S. rubroviolaceous*	6	<3	—	—	<5	Kaunda-Arara & Rose (2004); Chateau & Wantiez (2008*b*); Meyer *et al.* (2010*a*); Welsh & Bellwood (2011); Colin (2012); Fox (2012)
Scarus ghobban	6	<3	—	—	<10	Chateau & Wantiez (2008*b*)
Calotomus carolinus	—	—	—	—	<5	Kaunda-Arara & Rose (2004)
Bolbometopon muricatum	20	<10	—	—	—	Hamilton (2004)
Scombridae (mackerel and tuna)						
Scomberomorus queenslandicus	—	—	—	—	<300 (<100)	Begg *et al.* (1997)
Scomberomorus cavalla	100	<50	—	—	—	Moe (1966)
Scomberomorus commerson and *S. munroi*	—	—	—	—	<2000 (<500)	Begg *et al.* (1997); Dunlop & Mann (2012)
Katsuwonus pelamis	—	—	—	—	<1000	Cayré (1991); Sibert & Hampton (2003); Dunlop & Mann (2012)

Table 1. Continued

CLASS Family (common name)	Recommended minimum marine reserve size (linear distance in km)	Movement (linear distance in km) Home range and territories	Spawning (breeding) migrations	Ontogenetic habitat shifts	Other long-term movements (core areas of use)	Sources
Thuunus obesus	—	—	—	—	<100 (<75)	Dagorn, Bach & Josse (2000)
Thunnus albacares	—	—	—	—	<3000 (<600)	Cayré (1991); Sibert & Hampton (2003); Dunlop & Mann (2012)
Thunnus thynnus	—	—	<7000	—	—	Wilson *et al.* (2005, 2011)
Thunnus maccoyii	—	—	~9000	—	—	Patterson *et al.* (2008)
Siganidae (rabbitfishes)						
Siganus lineatus	2	<1	—	—	—	Fox & Bellwood (2011); Fox (2012)
Siganus doliatus and *S. fuscescens*	6	<3	—	—	—	Bellefleur (1997); Fox (2012)
Siganus sutor	10	—	<5	—	<30 (<5)	Kaunda-Arara & Rose (2004); Samoilys *et al.* (2013)
Sphyraenidae (barracudas)						
Sphyraena jello	20	—	—	—	<50 (<10)	Dunlop & Mann (2012)
Sphyraena barracuda	40	—	—	—	<200 (<20)	Springer & McErlean (1961) in O'Toole *et al.* (2011); O'Toole *et al.* (2011); Dunlop & Mann (2012)
Sygnathidae (seahorses)						
Hippocampus bargibanti and *H. comes*	<0.1	<0.02	—	—	—	Perante *et al.* (2002); Baine *et al.* (2008)
Hippocampus reidi	0.4	<0.2	—	—	—	Rosa, Dias & Baum (2002); Freret-Meurer & Andreata (2008)
Xiphiidae (swordfishes)						
Xiphias gladius	—	—	—	—	1000s	Takahashi *et al.* (2003)
CHONDRICHTHYES						
Carcharhinidae (requiem sharks)						
Carcharhinus brevipinna and *C. leucas*	—	—	—	—	<20	Stevens, West & McLoughlin (2000); Yeiser, Heupel & Simpfendorfer (2008)

Table 1. Continued

CLASS Family (common name)	Recommended minimum marine reserve size (linear distance in km)	Movement (linear distance in km): Home range and territories	Spawning (breeding) migrations	Ontogenetic habitat shifts	Other long-term movements (core areas of use)	Sources
Carcharhinus albimarginatus	—	—	—	—	<20 (<2)	Kato & Carvallo (1967) in Stevens (1984); Stevens (1984); Barnett *et al.* (2012)
Carcharhinus perezi	—	<40	—	—	<40 (<10)	Kohler, Casey & Turner (1998); Chapman *et al.* (2005); Garla *et al.* (2006); Bond *et al.* (2012)
Rhizoprionodon acutus and *R. taylori*	—	—	—	—	<100	Stevens *et al.* (2000); Yeiser *et al.* (2008)
Carcharhinus amblyrynchoides, *C. falciformis* and *C. fitroyensis*	—	—	—	—	<200	Kato & Carvallo (1967) in Stevens (1984); Stevens (1984); Stevens *et al.* (2000)
Carcharhinus plumbeus	—	<200	—	—	—	Rechisky & Wetherbee (2003)
Carcharhinus melanopterus	—	<20	<50	<100	<200 (<10)	Stevens (1984); Papastamatiou *et al.* (2009, 2010); Dunlop & Mann (2012); Chin *et al.* (2012, 2013*a*,*b*); (J. Mourier, unpublished data) in Mourier & Planes (2013); Mourier & Planes (2013)
Carcharhinus amblyrhynchus	—	<10	—	—	<200 (<20)	McKibben & Nelson (1986); Heupel, Simpefendorfer & Fitzpatrick (2010); Barnett *et al.* (2012); (Speed *et al.*, personal communication) in Field *et al.* (2011); Field *et al.* (2011); Vianna *et al.* (2013)
Carcharhinus amboinensis	—	<30	—	—	<300 (<20)	Stevens *et al.* (2000); Knip *et al.* (2011); Dunlop & Mann (2012)
Carcharhinus macloti	—	—	—	—	<800 (<50)	Stevens *et al.* (2000)
Carcharhinus sorrah	—	<20	—	—	<2000 (<50)	Stevens (1984); Knip, Heupel & Simpfendorfer (2012*a*,*b*)
Carcharhinus tilsoni	—	—	—	—	<2000 (<50)	Stevens (1984)
Carcharhinus galapagensis	—	—	—	—	<3000 (<100)	Kohler *et al.* (1998); Lowe *et al.* (2006); Meyer, Papastamatiou & Holland (2010*b*)
Carcharhinus limbatus and *C. longimanus*	—	—	—	—	<3000	Kohler *et al.* (1998); Heupel, Simpfendorfer & Hueter (2004); DeAngelis *et al.* (2008)

Table 1. Continued

CLASS		Movement (linear distance in km)				
Family (common name)	Recommended minimum marine reserve size (linear distance in km)	Home range and territories	Spawning (breeding) migrations	Ontogenetic habitat shifts	Other long-term movements (core areas of use)	Sources
Galeocerdo cuvier	—	<35	—	—	<8000 (<500)	Kohler *et al.* (1998); Holland *et al.* (1999); Stevens *et al.* (2000); Lowe *et al.* (2006); Heithaus *et al.* (2007); Meyer *et al.* (2009, 2010*b*); Dunlop & Mann (2012)
Negaprion acutidens and *N. brevirostris*	—	<5	—	—	<1000 (<2)	Stevens (1984); Gruber, Nelson & Morrissey (1988); Morrissey & Gruber (1993); Kohler *et al.* (1998); Feldheim, Gruber & Ashley (2001); Wetherbee, Gruber & Rosa (2007); DeAngelis *et al.* (2008); Yeiser *et al.* (2008)
Triaenodon obesus	—	<10	—	—	<30 (<10)	Randall (1977); Barnett *et al.* (2012); Whitney *et al.* (2012)
Ginglymostomatidae (nurse sharks)						
Nebrius ferrugineus	—	—	—	—	<50	Stevens *et al.* (2000)
Ginglymostoma cirratum	—	—	—	—	<600 (<10)	Kohler *et al.* (1998); Chapman *et al.* (2005)
Myliobatidae (eagle and manta rays)						
Manta alfredi	—	<50	—	—	<500	Clark (2010); Couturier *et al.* (2011)
Manta birostris	—	<40	—	—	<200	Dewar *et al.* (2008); Graham *et al.* (2012)
Rhinoptera bonasus	—	—	—	—	<20 (<2)	Collins, Heupel & Motta (2007)
Pristidae (sawfishes)						
Pristis pectinata	—	—	—	—	<20	Simpfendorfer, Wiley & Yeiser (2010)
Rhincodontidae (whale sharks)						
Rhincodon typus	—	—	—	—	<2000–<13000	Wilson *et al.* (2006); Eckert & Stewart (2001)
Sphyrnidae (hammerhead sharks)						
Sphyrna leweni and *S. tiburo*	—	<10	—	—	<200	Holland *et al.* (1993*b*); Klimley (1993); Stevens *et al.* (2000); Heupel *et al.* (2006); Hearn *et al.* (2010)
Eusphyra blochi	—	<20	—	—	—	Stevens *et al.* (2000)
Sphyrna mokarran	—	—	—	—	<400	Stevens *et al.* (2000)

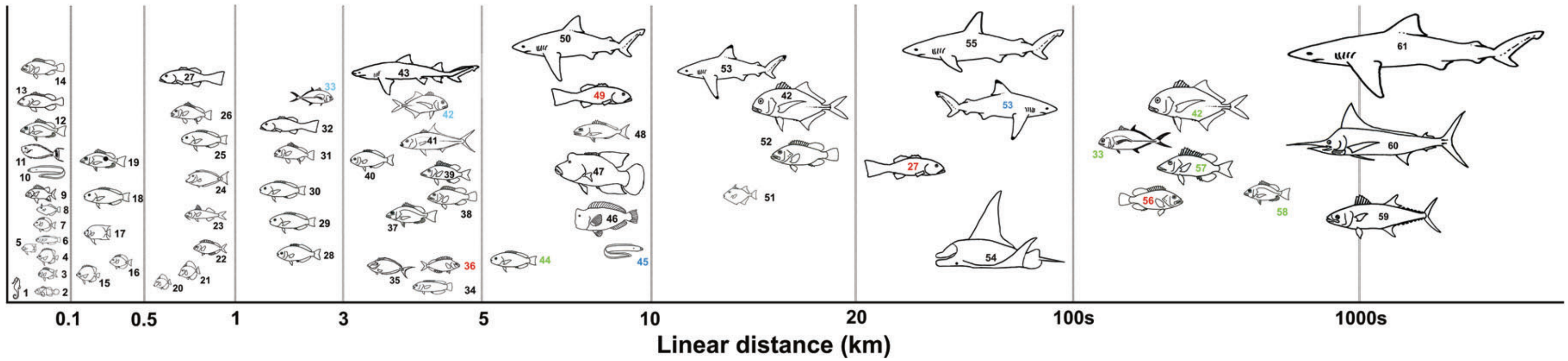

Fig. 1. Linear scale of movement of coral reef and coastal pelagic fish species (modified from Maypa, 2012). Number colours are: black (daily movements: home ranges, territories and core areas of use); blue (ontogenetic shifts); red (spawning migrations); and green (long-term movements of undetermined cause). 1, Seahorses (*Hippocampus* spp.); 2, anemonefishes (*Amphiprion* spp.); 3, most damselfishes (e.g. *Dascyllus* spp.); 4, most butterflyfishes (*Chaetodon* spp.); 5, some angelfishes (e.g. *Centropyge* spp.); 6, some wrasses (e.g. *Halichoeres garnoti*); 7, some surgeonfishes (e.g. *Acanthurus lineatus*); 8, orangespotted filefish (*Cantherhines pullus*); 9, some soldierfishes/squirrelfishes (*Holocentrus* spp./*Myripristis* spp.); 10, moray eels (*Gymnothorax spp.*); 11, bignose unicornfish (e.g. *Naso vlamingii*); 12, some snappers (e.g. *Lutjanus carponotatus*); 13, some groupers (most *Cephalopholis* spp.); 14, some groupers (*Ephinephelus* spp.); 15, some butterflyfishes (e.g. *C. striatus*); 16, some surgeonfishes (e.g. *A. coeruleus* and *Ctenochaetus striatus*); 17, some angelfishes (*Holocanthus/Pomacanthus* spp.); 18, some parrotfishes (some *Scarus/Sparisoma* spp.); 19, some snappers (e.g. *L. ehrenbergii*); 20, yellow tang (*Zebrasoma flavescens*); 21, twotone tang (*Z. scopas*); 22, some rabbitfishes (e.g. *Siganus lineatus*); 23, goatfishes; 24, bluespine unicornfish (*N. unicornis*); 25, some parrotfishes (e.g. *Scarus rivulatus*); 26, some grunts (e.g. *Haemulon sciurus*); 27, squaretail coralgrouper (*Plectropomus areolatus*); 28, Bermuda sea chub (*Kyphosus sectatrix*); 29, some parrotfishes (*Chlorurus* spp.); 30, ember parrotfish (*S. rubroviolaceus*); 31, goldspotted sweetlip (*Plectorhinchus flavomaculatus*); 32, some groupers (e.g. *P. leopardus*); 33, bigeye trevally (*Caranx sexfasciatus*); 34, some wrasses (e.g. *Coris aygula*); 35, some surgeon/unicornfishes (e.g. *A. blochii* and *N. lituratus*); 36, shoemaker spinefoot (*S. sutor*); 37, red snapper (*L. campechanus*); 38, some groupers (e.g. *C. sonnerati* and *E. coicoides*); 39, some emperors (e.g. *Lethrinus nebulosus*); 40, silver drummer (*Kyphosus sydneyanus*); 41, kingfishes (*Seriola* spp.); 42, giant trevally (*C. ignobilis*); 43, lemon sharks (*Negaprion* spp.); 44, blue-barred parrotfish (*S. ghobban*); 45, Indonesian shortfin eel (*Anguilla bicolor bicolor*); 46, bumphead parrotfish (*Bolbometopon muricatum*); 47, humphead wrasse (*Cheilinus undulatus*); 48, green jobfish (*Aprion virescens*); 49, leopard coralgrouper (*P. leopardus*); 50, whitetip reef shark (*Triaenodon obesus*) and nurse shark (*Ginglymostoma cirratum*); 51, grey triggerfish (*Balistes capriscus*); 52, gag grouper (*Mycteroperca microlepis*); 53, blacktip reef shark (*Carcharhinus melanopterus*); 54, manta rays (*Manta* spp.); 55, Galapagos shark (*C. galapagensis*); 56, Nassau grouper (*E. striatus*); 57, trumpet emperor (*L. miniatus*); 58, mangrove red snapper (*L. argentimaculatus*); 59, tuna; 60, marlin/swordfish; 61, tiger shark (*Galeocerdo cuvier*). Most illustrations were modified from Randall, Allen & Steene (1997), *B. muricatum* was modified from Gladstone (1986) and some were drawn by A.P. Maypa. Table 1 provides specific values and additional species.

values to maximum linear distance in kilometres (between movement boundaries in the longest dimension) because the asymmetrical shape of some home ranges (Kramer & Chapman, 1999) made converting distances to area more problematic. Where only areal measurements were provided, we either obtained maximum linear distances from the authors or measured them from figures in papers. Where this was not possible, we converted areas to linear distance using the formulae for a circle or square (modified from Kramer & Chapman, 1999) for species where home ranges are small relative to patches of appropriate habitat (e.g. for *Sparisoma* spp.: Mumby & Wabnitz, 2002).

(1) Home ranges

The home range of a fish is the area in which an individual spends the majority of its time and engages in most of its routine activities including foraging and resting (Kramer & Chapman, 1999; Botsford *et al.*, 2009*a*; Gruss *et al.*, 2011). Many species also undertake regular movements to and from resident spawning aggregations (e.g. parrotfishes, wrasses and surgeonfishes: Claydon, 2004; Domeier, 2012), which are considered to be within the home range of participating individuals (Kramer & Chapman, 1999). Larger scale movements to transient spawning aggregations are considered to be spawning migrations outside their home ranges (see Section II.2 for definitions).

(*a*) *Factors influencing home range size*

Home range size varies among and within species (Table 1), and is influenced by a range of factors (Kramer & Chapman, 1999; Speed *et al.*, 2010; Gruss *et al.*, 2011). Movement distances generally increase with increasing body size, with larger species (and individuals) tending to exploit wider areas and greater distances than smaller ones (Kramer & Chapman, 1999; Palumbi, 2004), probably because larger individuals need more space to provide enough resources to accommodate their greater energetic requirements and range of behaviours (Speed *et al.*, 2010; Gruss *et al.*, 2011). For example, Knip *et al.* (2011) found that older sharks (*Carcharhinus amboinensis*) used larger areas and undertook more excursions from their home ranges than younger ones. However there are some exceptions, for example some jacks (e.g. *Caranx ignobilis* and *C. melampygus*) undertake long-distance excursions of tens to hundreds of kilometres (Tagawa & Tam, 2006; Dunlop & Mann, 2012), but adults tend to use core areas <5–10 km long (Holland, Lowe & Bradley, 1996; Meyer, Holland & Papastamatiou, 2007*a*).

Habitat characteristics such as reef type, structure, size and shape can also influence movement patterns (Kramer & Chapman, 1999; Gruss *et al.*, 2011), where home ranges are likely to be smaller for species in habitats with more available food and shelter compared to habitats where food and shelter are scarce (Gruss *et al.*, 2011). For example in the Caribbean, Semmens, Brumbaugh & Drew (2005) found that due to differences in the amount and distribution of resources, surgeonfish (*Acanthurus coeruleus*) territories are larger in areas of reef pavement (that have low biogenic structure) than in areas of reef crest (that have high biogenic structure). Similarly, Zeller (1997) found that the influence of reef type and shape are reflected in the home ranges of a coral grouper (*Plectropomus leopardus*) on the Great Barrier Reef, i.e. home ranges on continuous fringing reefs are significantly smaller than on isolated patch reefs.

Some coral reef species also make crepuscular movements on a daily basis between daytime resting areas and nightime feeding areas (Kramer & Chapman, 1999). Often, these activities occur in different habitat types, and the home range consists of two areas joined by a narrow movement path. For example, in the Caribbean, many species of grunt (*Haemulon* spp.) rest during the day on coral reefs and move tens to hundreds of metres to feed over soft substrata at night (Burke, 1995; Beets *et al.*, 2003). Since some species may move long distances between resting and feeding habitats (e.g. the emperor *Lethrinus nebulosus* moves up to 1 km between lagoon patch reefs and soft bottoms each day: Chateau & Wantiez, 2008*b*), they sometimes have home ranges that are larger than species whose home ranges include only one habitat type (Kramer & Chapman, 1999).

Some species also exhibit movement patterns in response to social organisation and behavioural life-history traits. Species and individuals that exhibit territoriality and intra- and interspecific aggression tend to have a strong attachment to sites, limiting their home range size (Afonso *et al.*, 2008). Territory size also varies among and within species, where size can be influenced by many factors including substrate rugosity, harem size and competition (Mumby & Wabnitz, 2002). Territory size may also differ between sexes. For example in species that live in harems composed of a dominant male and several females, males have larger territories than females (Shpigel & Fishelson, 1991; Sakai & Kohda, 1995).

Fish movement patterns are also influenced by density-dependent factors (reviewed in Gruss *et al.*, 2011), including where they are driven by positive or negative interactions with conspecifics or species belonging to the same guild (e.g. the unicornfish *Naso vlamingii* moves away from conspecifics in high-density areas: Abesamis & Russ, 2005) or where species exhibit movements in response to the density of their prey or predators (Hixon & Carr, 1997).

Home range size in some species also varies with season, tide and time of day (Meyer *et al.*, 2007*a*; Speed *et al.*, 2010; Barnett *et al.*, 2012). For example, many shark species tend to have small daytime home ranges and use larger areas at night, while others make seasonal migrations related to prey movements and environmental gradients (reviewed in Speed *et al.*, 2010). Juvenile snappers and emperors also use different habitats in different seasons or tidal phases (Dorenbosch *et al.*, 2004; Mellin, Kulbicki & Ponton, 2007).

(*b*) *General patterns in home range size among taxa and trophic groups*

Some fishes are found predominantly in and around coral reef environments (including associated sand, rubble and rocky areas) and depend on coral reefs for food and/or shelter

(Bellwood, 1988). The scale of home range movements of these species is highly variable among and within families (Table 1 and Fig. 1, for further details see online Appendix S1).

Some coral reef fishes have very small home ranges (<10–20 m long) that are limited to one site or habitat. They tend to include very small species such as cardinalfishes, gobies, some seahorses, most damselfishes and some angelfishes (e.g. *Centropyge ferrugatus*). Some small- to medium-sized coral reef species also have small home ranges or territories (<0.1 km long) including most butterflyfishes, soldierfishes, squirrelfishes and filefishes (e.g. *Cantherhines pullus*), while others move further (but still <0.5 km) such as some butterflyfishes and angelfishes (e.g. *Chaetodon striatus* and *Pomacanthus paru*: Chapman & Kramer, 2000).

Herbivorous reef fishes show a variety of movement patterns. Some surgeonfishes (e.g. *Acanthurus lineatus*), parrotfishes (e.g. *Sparisoma* spp.) and damselfishes (e.g. *Pomacentrus* spp.) are territorial, and aggressively defend feeding or breeding territories that range from <1 to ~20 m across. Others form roving schools or have home ranges that include movements between nocturnal shelters, feeding and spawning sites (e.g. the surgeonfish *A. nigrofuscus*: Mazeroll & Montgomery, 1995). Home range sizes for most surgeonfishes and unicornfishes are <0.3–1 km long, although some are several kilometres long (e.g. for *A. nigrofuscus* and *Naso lituratus*). Similarly most parrotfishes do not move very far (<0.1–0.5 km for most *Sparisoma* spp., and small *Scarus* and *Chlorurus* species), although some have home ranges up to 3 km across (e.g. some larger *Chlorurus* and *Scarus* species). The largest parrotfish species, *Bolbometopon muricatum*, may move up to 10 km a day (Hamilton, 2004).

Home ranges for other herbivores such as sea chubs (*Kyphosus* spp.) have also been recorded to extend up to 3–5 km across. By contrast, most rabbitfishes have home ranges <3 km long, with at least one species (*Siganus sutor*) moving long distances (30 km) including undertaking confirmed spawning migrations >3 km long (Samoilys *et al.*, 2013).

Coral reef piscivores such as groupers also show a variety of movement patterns. Some species are sedentary and have small home ranges or territories <100 m long (e.g. most *Cephalopholis* and some *Epinephelus* species), while others may have home ranges several kilometres across (e.g. some *Epinephelus* and *Plectropomus* species). A few species also undergo long-distance spawning migrations of tens to hundreds of kilometres (e.g. *E. fuscoguttatus* and *E. striatus*: see Section II.2).

Variation in home range size is also apparent in other coral reef predators. Although few studies have focused on movement patterns of wrasses, home range sizes seem to vary with body size with small- to moderate-sized species and individuals having small home ranges <100 m across (e.g. *Thalassoma bifasciatum* and *Bodianus rufus*), larger species having home ranges several kilometres long (e.g. *Coris aygula*), and the largest species having home ranges up to 10 km long (*Cheilinus undulatus*). By comparison, movement patterns of goatfishes do not vary much, with most species having home ranges <0.5–1 km long (e.g. *Mulloidichthys* and *Parupeneus* species).

Many other large predatory fishes that are highly mobile or nomadic (Gruss *et al.*, 2011) are also typically found in association with coral reefs (Bellwood, 1988), including some species of jack, barracuda, snapper, emperor and sweetlip. However, while many of these species range over large distances (tens, hundreds and thousands of kilometres), some exhibit site fidelity within core areas <5–10 km across including some jacks (e.g. *Caranx ignobilis*), barracuda (e.g. *Sphyraena jello*), snappers (e.g. *Aprion virescens*), emperors (e.g. *Lethrinus mahsena*) and sweetlips (e.g. *Plectorhinchus flavomaculatus*).

Other snappers show a wide range of movement patterns. Some species that are closely associated with coral reefs have small home ranges (e.g. <100 m across for *Lutjanus carponotatus*), while others have home ranges up to several kilometres long (e.g. *L. johni*). Others move long distances (e.g. tens to hundreds of kilometres), which may represent ontogenetic shifts in habitat or spawning migrations (e.g. for *L. argentimaculatus* and *L. campechanus*).

Coral reef and coastal pelagic sharks (e.g. some requiem, nurse and hammerhead sharks) have complex movement patterns that vary with species, size, reproductive status, ontogeny, tide, time of day, prey availability and environmental conditions (reviewed by Speed *et al.*, 2010). Fidelity to sites <5–10 km long is common in species that use nursery areas (e.g. *Carcharhinus amblyrhynchos* and *Negaprion brevirostris*), although some individuals make longer excursions that extend far beyond their usual home ranges (e.g. >100 km for *C. amblyrhynchos* and up to 1000 km for *N. brevirostris*: Speed *et al.*, 2010). Site fidelity to mating, feeding and natal sites may be less common, and has only been observed in a few species (e.g. *Carcharhinus melanopterus* moves up to 50 km to specific pupping areas in French Polynesia: Mourier & Planes, 2013). By contrast, large coastal and oceanic sharks have been recorded to move 1000s of kilometres (e.g. *Carcharhinus limbatus* and *Carcharhinus longimanus*) with some undergoing transoceanic migrations (e.g. *Galeocerdo cuvier* and *Rhincodon typus*), which may be a result of changing reproductive status or shifting prey distribution (Speed *et al.*, 2010). Manta rays (*Manta* spp.) also show fidelity to areas <50 km across (e.g. Clark, 2010), with excursions that extend hundreds of kilometres beyond their home range.

Pelagic species (that may be found in the proximity of reefs, but which principally occur in open water and have no direct dependence on reefs for food or shelter) also typically move over very large (10–100 km) or huge distances (hundreds to thousands of kilometres) including mackerel and tuna (e.g. *Scomberomorus* and *Thunnus* species), dolphinfish (*Coryphaena hippurus*), billfishes (e.g. *Makaira* spp.) and swordfishes (e.g. *Xiphias gladius*). These large-scale movements are most likely part of ontogenetic and/or seasonal migrations for feeding and breeding (e.g. *Thunnus maccoyii* move up to 9000 km between feeding and breeding grounds: Patterson *et al.*, 2008). Despite many pelagic species moving long distances, some species (or individuals) use more limited areas. For example, Begg, Cameron & Sawynok (1997) found that while school mackerel (*Scomberomorus queenslandicus*) move up to 270 km, most individuals move less than 50 km.

(2) Spawning migrations

Spawning migrations represent the movement of fish from their home range to a spawning site. For many coral reef fish species, the end result of a spawning migration is the formation of a (fish) spawning aggregation (FSA), which by definition is a group of conspecific fishes, gathered specifically for the purpose of spawning, with densities typically four times (or more) that found in non-reproductive periods (Domeier, 2012; also see Sadovy de Mitcheson & Colin, 2012, for a complete review). To date, 119 species from 18 different fish families are known to form spawning aggregations (Choat, 2012; www.scrfa.org). FSAs may be comprised of a number of species, while individual sites may entertain multiple species simultaneously or sequentially over time.

FSAs are predictable events that occur at highly specific times and locations, making them particularly susceptible to overfishing (Sadovy & Domeier, 2005; Rhodes & Tupper, 2008; Domeier, 2012). Recent evidence indicates that at least some FSA-forming species of coral reef fishes utilise common migratory corridors preceding or following reproduction (e.g. Starr *et al.*, 2007; Rhodes & Tupper, 2008; Rhodes *et al.*, 2012). Subgroups of reproductively active fish may also form at nearby staging areas prior to and after migration to FSA sites (Nemeth, 2012). Similar to the actual FSA, both reproductive migratory corridors and staging areas concentrate reproductively active fish in a manner that enhances the potential for removal of individuals prior to spawning.

FSAs generally fall within two primary categories: resident and transient, which differ in the frequency of occurrence, persistence of the aggregation, site specificity and the relative distance that fish migrate to reach the site. Resident spawners tend to spawn frequently throughout the year and travel short distances (metres to hundreds of metres) to spawning sites nearby, which are considered part of their home range (see Section II.1). As such, resident spawners are less likely to be impacted by fisheries when their home ranges are enclosed in a marine reserve. Resident spawners primarily include herbivorous and omnivorous fishes, such as parrotfishes, surgeonfishes and wrasses (Colin, 2012).

By contrast, transient spawners often travel long distances (kilometres to hundreds of kilometres) over days or weeks to reach specific spawning sites outside of their home range (Domeier, 2012: Table 1 and Fig. 1, for additional details see online Appendix S1). More often than not, transient spawners include large-bodied and commercially important fishes, such groupers, snappers, emperors and rabbitfishes. Spawning sites for transient spawners tend to be concentrated on or near shelf edges, whereas resident spawning aggregations may also occur in inshore areas (Claydon, 2004; Colin, 2012). Transient spawners tend to have relatively short reproductive seasons compared with resident spawners, with actual spawning confined to one or a few days toward the end of the aggregation period. Between spawning periods, fish participating in transient spawning aggregations often travel back to their home ranges only to return to the FSA site during subsequent reproductive events, which may be as long as 1 year or as short as several days away. Since these migrations are often extensive, fish may be drawn away from marine reserves where they become subject to the fishery (e.g. Rhodes & Tupper, 2008; Rhodes *et al.*, 2012). For both resident and transient aggregations, the area from which fish are drawn to reproductive sites is referred to as the catchment area, and no fishing in this area is often considered necessary to fully protect FSA-forming species.

(3) Ontogenetic habitat shifts

Some coral reef fishes undergo ontogenetic shifts where they use different habitat types (e.g. mangroves and seagrasses) as nursery grounds before moving to their adult habitat on coral reefs (e.g. some parrotfishes, grunts, snappers, surgeonfishes, jacks, barracuda, emperors, groupers, goatfishes, wrasses and rabbitfishes: Smith & Parrish, 2002; Mumby *et al.*, 2004; Nagelkerken, 2007). Many shark species also undergo ontogenetic habitat shifts (reviewed in Speed *et al.*, 2010; Chin *et al.*, 2013*a*). For instance, some coastal shark species use shallow turbid waters in bays or rivers as nursery habitats before moving offshore into deeper, clearer adult habitats (e.g. some requiem and hammerhead sharks: Holland *et al.*, 1993*b*; Simpfendorfer & Milward, 1993; Knip *et al.*, 2011).

Other species use different depths, zones or habitats on coral reefs at different stages in their life histories (e.g. some jacks, butterflyfishes, surgeonfishes and sharks: Wetherbee *et al.*, 2004; Claisse *et al.*, 2009; Maypa, 2012). For example, some butterflyfishes prefer shallow coral reef habitats as juveniles, while adults are more widely distributed throughout a range of depths (e.g. *Chaetodon auriga*: Pratchett *et al.*, 2008). Several studies have also documented ontogenetic shifts among coral reef habitats to fully protect sharks. For example, Papastamatiou *et al.* (2009) found that juvenile blacktip reef sharks (*Carcharhinus melanopterus*) show stronger selection for shallow sand flats while adults prefer reef ledges.

These ontogenetic shifts in habitat use have been hypothesised as a trade-off between mortality risk and growth or foraging rate, and may also reflect a change in diet preferences with age, a mechanism to reduce intraspecific predation or competition, or changes in reproductive status (e.g. Dahlgren & Eggleston, 2000; Mumby *et al.*, 2004; Nagelkerken, 2007; Speed *et al.*, 2010). For example, the surgeonfish *Zebrasoma flavescens* initially settle in deeper, structurally complex coral-rich habitats that offer protection from predation, then shift to a habitat with less shelter and more food as they grow (Ortiz & Tissot, 2008; Claisse *et al.*, 2009).

These ontogenetic shifts in habitat have important consequences for the structure of coral reef fish assemblages and populations of key species (Nagelkerken, 2007). For example, Mumby *et al.* (2004) demonstrated that the presence of juvenile habitat (mangroves) in the vicinity of coral reefs exerts a profound impact on community structure by elevating the adult biomass of several species of parrotfishes, grunts and snappers on reefs in the Caribbean (see also Nagelkerken, 2007). Several studies in the Indo-Pacific have also demonstrated that some wrasses, parrotfishes, snapper, grouper and sweetlips are either absent or have lower adult densities on coral reefs where their juvenile habitats (mangroves, seagrasses or sheltered lagoonal, backreef or inshore reefs) are lacking (e.g. Adam *et al.*, 2011; Olds *et al.*, 2012; Wen *et al.*, 2013). Coral reef species that depend on juvenile habitats for population maintenance include three species listed as Near Threatened, Endangered or Vulnerable on the IUCN Red List (www.iucnredlist.org): the humphead wrasse *Cheilinus undulatus*; the bumphead parrotfish *Bolbometopon muricatum*; and the rainbow parrotfish *Scarus guacamaia* (Mumby *et al.*, 2004; Dorenbosch *et al.*, 2005, 2006; Hamilton & Choat, 2012).

With some exceptions (e.g. Verweij *et al.*, 2007; Papastamatiou *et al.*, 2009; Chin *et al.*, 2013*a*), our understanding of these habitat shifts is generally based on indirect evidence from studies comparing density and size distributions of species in different habitats rather than empirical measurements of movement patterns of key species (e.g. Smith & Parrish, 2002; Simpfendorfer *et al.*, 2005; reviewed in Nagelkerken, 2007). While empirical evidence of ontogenetic shifts in habitat use is limited, some studies provide useful insights into the spatial scale of these movements (Table 1 and Fig. 1, for additional details see online Appendix S1). For example, the best available information suggests that some snappers and damselfishes have ontogenetic shifts of <10–100s of metres (e.g. *Lutjanus apodus* and *Dascyllus aruanus*), while some jacks (e.g. *Caranx ignobilis* and *C. sexfasciatus*) and grunts (*Haemulon flavlineatum*) undergo ontogenetic shifts of more than 2–3 km (e.g. Maypa, 2012). Other species undergo much larger scale movements. For example juvenile blackspot snapper (*Lutjanus ehrenbergii*) and blacktip reef sharks (*Carcharhinus melanopterus*) move more than 30 and 80 km respectively between coastal nursery habitats and reefs (McMahon, Berumen & Thorrold, 2012; Chin *et al.*, 2013*a*).

III. LARVAL DISPERSAL

How far larvae disperse clearly has important consequences for designing effective reserves and reserve networks. In the last few decades, research on larval dispersal in coral reef fishes has advanced rapidly. Since the last review of this topic by Jones *et al.* (2009), a number of new empirical studies have shed more light on the spatial scale of larval dispersal, including the first studies of fishery species (Table 2). These new studies have taken advantage of methodological and technological innovations in the field of genetics (e.g. Planes *et al.*, 2009; Puebla, Bermingham & Guichard, 2009; Pinsky, Montes & Palumbi, 2010) to quantify how far larvae disperse from their parents during the pelagic larval phase.

Despite substantial progress made during the past decade, our understanding of the extent of larval dispersal, and how to use this information to inform marine reserve design, remains preliminary. For example, population persistence within a marine reserve or a network of reserves depends upon recruitment to the local population, through local retention (the proportion of larvae that return to their natal origin) and other connectivity pathways (Botsford *et al.*, 2009*b*; Burgess *et al.*, 2014). However, while local retention is the appropriate metric to use to assess the contribution of local production to population persistence (Burgess *et al.*, 2014), this is difficult (almost impossible?) to estimate empirically given that the destination of all larvae produced at a particular location must be known (Botsford *et al.*, 2009*b*). Instead, most studies have measured self-recruitment (i.e. the proportion of recruits that are the offspring of parents in the same population), which represents an unknown proportion of local production. As such, the information on larval dispersal synthesised here represents the best information currently available to inform decisions about the design of marine reserve networks. Our recommendations based on this information (see Section IV.1) should be reviewed and refined as further empirical results emerge.

In order to develop guidelines for spatial management, we sought to infer from available studies the minimum, maximum and average larval dispersal distances for a range of species. Our objective was to provide a general idea (based on empirical evidence from 14 species in 12 studies: Table 2) of: how far larvae usually settle from natal populations during single-generation dispersal events; the consistency of these dispersal patterns across species and through time; and the probable shape of the dispersal kernel (the likelihood of successful dispersal as a function of distance from a source population).

It is important to note that the relatively few available studies employed different methodological approaches to measure larval dispersal including larval tagging, genetic parentage analysis, genetic isolation-by-distance and genetic assignment (Table 2). Each of these methods has its strengths and weaknesses. For example, larval tagging and genetic parentage analysis can provide unequivocal empirical measurements of larval dispersal but may underestimate average dispersal distance because the large sample sizes required by this approach limit its application to relatively small spatial scales (tens of kilometers). Genetic isolation-by-distance methods, on the other hand, can be used across considerably larger spatial scales (hundreds to thousands of kilometers), but they require knowledge about the effective population size (conceptualised as the number of individuals in a population that contribute offspring to the next generation), which is difficult to estimate empirically (Pinsky *et al.*, 2010). For consistency with other metrics reported herein (see Section II), where empirical measurements of dispersal were reported as the size of the area occupied by the source population (such as in measurements of % self-recruitment within a particular area), we have converted these to a linear measure by assuming that the area in question is a circle.

Table 2. Summary of larval dispersal of coral reef fishes.

Family	Location (habitat type)^{method}	Egg type	Planktonic larval duration (days)	Source population area (ha)	% self-recruitment	Mean (min–max) observed dispersal (km)	Year	Source
Chaetodontidae								
Chaetodon capistratus	Central American Caribbean coast (continuous; barrier reef)^{GID}	Pelagic	20–57	212500	n.e.	41.9 (?–?)	—	Puebla *et al.* (2012)
Chaetodon vagabundus	Kimbe Bay, Papua New Guinea (patchy; mixed)$^{LT, GP}$	Pelagic	29–48	47	52–72	n.e. (<1– < 1)	1	Almany *et al.* (2007)
			—	47	32–47	n.e. (<1–33)	2	Berumen *et al.* (2012)
Epinephelidae								
Hypoplectrus nigricans	Central American Caribbean coast (continuous; barrier reef)^{GID}	Pelagic	13–22	182500	n.e.	7.7 (?–?)	—	Puebla *et al.* (2012)
Hypoplectrus puella	Central American Caribbean coast (continuous; barrier reef)^{GID}	Pelagic	~21*	multiple	n.e.	2.3–14.4 (?–?)	—	Puebla *et al.* (2009)
Plectropomus areolatus	Manus Island, Papua New Guinea (continuous; coastal)^{GP}	Pelagic	(19–31)†	563	15–21	14.4 (2.8–33)	—	Almany *et al.* (2013)
Plectropomus maculatus	Keppel Islands, Australia (patchy; island archipelago)^{GP}	Pelagic	24–29	36	0	8.6 (0.2–28)	—	Harrison *et al.* (2012)
			—	60	9	—	—	Harrison *et al.* (2012)
Labridae								
Thalassoma bifasciatum	Central American Caribbean coast (continuous; barrier reef)^{GID}	Pelagic	38–94	212500	n.e.	21.8 (?–?)	—	Puebla *et al.* (2012)
Haemulidae								
Haemulon flavolineatum	Central American Caribbean coast (continuous; barrier reef)^{GID}	Pelagic	13–20	212500	n.e.	37 (?–?)	—	Puebla *et al.* (2012)
Lutjanidae								
Lutjanus carponotatus	Keppel Islands, Australia (patchy; island archipelago)^{GP}	Pelagic	21–27	36	14	7.4 (0.2–28)	—	Harrison *et al.* (2012)
			—	60	16	—	—	

Table 2. Continued

Family	Location (habitat type)^{method}	Egg type	Planktonic larval duration (days)	Source population area (ha)	% self-recruitment	Mean (min–max) observed dispersal (km)	Year	Source
Pomacentridae								
Amphiprion chrysopterus	Moorea, French Polynesia (continuous; coastal)^{GP}	Benthic	~17	674	54	n.e.	1	Beldade *et al.* (2012)
		—	—	674	32	n.e.	2	
Amphiprion clarkii	Leyte & Cebu Islands, Philippines (continuous; coastal)^{GID}	Benthic	7–11	Multiple	n.e.	8.8 (?–?)	—	Pinsky *et al.* (2010)
Amphiprion percula	Kimbe Bay, Papua New Guinea (patchy; mixed)$^{LT, GP}$	Benthic	10–13	47	42	n.e. (?–33)	1	Planes *et al.* (2009)
			—	47	60	n.e. (<1– < 1)	2	Almany *et al.* (2007)
			—	47	65	n.e. (?–25)	3	Berumen *et al.* (2012)
Amphiprion polymnus	Kimbe Bay, Papua New Guinea (patchy; coastal)$^{LT, GP}$	Benthic	9–12	20	16	Unknown	1	Jones *et al.* (2005)
			—	50	32	n.e. (0.1–?)	2	
	Bottless Bay, Papua New Guinea (patchy; coastal)^{GP}		—	3200	18	5.1 (0.015–27.2)	1	Saenz-Agudelo *et al.* (2012)
			—	3200	22	4.8 (0.015–35.6)	2	
			—	3200	23	5.2 (0.015–27.2)	3	
Stegastes partitus	Central American Caribbean coast (mixed; mixed)^{GA}	Benthic	24–40	>187000	22	46.9 (0.06–187)	1	Hogan *et al.* (2012)
			—	>187000	15	58.9 (0.06–187)	2	
			—	>187000	14	72.9 (0.06–187)	3	
	Central American Caribbean coast (continuous; barrier reef)^{GID}		—	212500	n.e.	7.5 (?–?)	—	Puebla *et al.* (2012)

GA, genetic assignment; GID, genetic isolation-by-distance; GP, genetic parentage; LT, larval tagging; n.e., not estimated.
*Wellington & Victor (1989).
†Planktonic larval duration of 19–31 days is from *P. leopardus* (see Doherty *et al.*, 1994).

Estimates of self-recruitment to small areas of known size provide an indication of the shortest distances that reef fish larvae disperse. Several studies that employed larval tagging and/or genetic parentage analysis on anemonefishes (*Amphiprion* spp.) and a butterflyfish (*Chaetodon vagabundus*) occupying areas of habitat with a diameter of 505–800 m (i.e. 20–50 ha) have recorded levels of self-recruitment ranging from 16 to 72% (Jones, Planes & Thorrold, 2005; Almany *et al.*, 2007; Planes *et al.*, 2009; Berumen *et al.*, 2012). By contrast, a genetic parentage study of two fishery species (the grouper *Plectropomus maculatus* and the snapper *Lutjanus carponotatus*) occupying two marine reserves with diameters of 677 m (36 ha) and 874 m (60 ha) recorded levels of self-recruitment ranging from 0 to 16% (Harrison *et al.*, 2012). In these studies, some larvae were recorded to have dispersed from as little as 10 m to several hundred metres from their parents (see also Buston *et al.*, 2012). Overall, evidence suggests that some reef fish larvae disperse very short distances, and that self-recruitment is common (see also Jones *et al.*, 2009).

At the other end of the spectrum, in the studies mentioned above on *Amphiprion*, *Chaetodon*, *Plectropomus* and *Lutjanus* species, the furthest larvae have been recorded to disperse is 28–36 km (which was as far as the authors sampled from the source populations: Table 2). However, reef fish larvae can and do disperse greater distances. For example, studies of the damselfish *Stegastes partitus* in the Caribbean (Hogan *et al.*, 2012, using genetic assignment: Table 2) and a subtropical species of wrasse, *Coris picta*, in Australia (Patterson & Swearer, 2007, using natural environmental markers in otoliths) provided evidence of larval dispersal to 187 and ~570 km, respectively. However, these long-distance dispersers are likely to represent the tail of the dispersal kernel. While long-distance dispersers are clearly important over evolutionary timescales, they are unlikely to constitute a significant source of population replenishment or connectivity over the ecological timescales that are the focus of fisheries management and the design of marine reserve networks.

Among the studies mentioned above, the genetic parentage analysis by Almany *et al.* (2013) on a spawning aggregation of a grouper (*Plectropomus areolatus*) in Papua New Guinea is the only one that could provide a quantitative description of the probable shape of the larval dispersal kernel of a fishery species over a spatial scale that is relevant to reserve networks. The study showed that the probability of successful larval dispersal (and therefore the number of settlers arriving at a site) declined rapidly as a function of distance from the source population. For instance, the dispersal kernel suggested that the magnitude of larval settlement >25 km from the source was <50% of the expected settlement at or very close to the source (0–5 km). The dispersal kernel also predicted that 50 and 95% of *P. areolatus* larvae settled within 13 and 33 km from the spawning aggregation, respectively. The dramatic decline in larval connectivity with distance was consistent with theoretical expectations (e.g. Siegel *et al.*, 2003; Cowen *et al.*, 2006) and the results of the only other empirical study of a reef fish (a non-fishery species) that estimated the shape of a dispersal kernel over a much smaller spatial scale (<1 km) (Buston *et al.*, 2012).

Several studies that followed Jones *et al.* (2009) sampled juveniles across a range of distances from the larval source(s), which can be used to estimate mean larval dispersal distance (Table 2). A number of studies sampled across a range of distances from source populations to a maximum distance of between 28 and 36 km, and used genetic parentage analysis to estimate mean larval dispersal ranging between 4.8 km in an anemonefish (*Amphiprion polymnus*: Saenz-Agudelo *et al.*, 2012) and 14.4 km in a coralgrouper (*Plectropomus areolatus*: Almany *et al.*, 2013). Perhaps sampling over greater distances would result in larger mean estimates. Two studies (Puebla *et al.*, 2009; Pinsky *et al.*, 2010) employing genetic isolation-by-distance methods on damselfishes (*Stegastes partitus* and *Amphiprion clarkii*) sampled across larger spatial scales (≥200 km), but provided mean dispersal estimates that are similar to those suggested by the studies using parentage analysis (Table 2). However, in one study using genetic assignment tests on *S. partitus* (Hogan *et al.*, 2012), mean dispersal was >10 times than in the aforementioned studies (Table 2). Although some studies have reported longer mean dispersal estimates, most recent studies suggest that, on average, larval dispersal in coral reef fishes across a variety of habitat configurations and life-history characteristics may be in the order of 5–15 km. Clearly, further studies on different species and in different habitat configurations would be useful in understanding to what extent this is true.

Another key question involving larval dispersal and the design of reserves and reserve networks is the degree of consistency in both self-recruitment and connectivity from 1 year to the next. Three recent studies measured connectivity and self-recruitment over 2 or 3 years (Table 2). Hogan *et al.* (2012) studied seven locations scattered across 187 km for the damselfish *Stegastes partitus*. They found that some self-recruitment occurred at each site in every year, but that the proportion of self-recruitment at a site varied among years, ranging from 0 (one site in 1 year) to 50%, with an overall site average of 15%. Similarly, connectivity among sites varied between years, but there was no evidence that the strength of connectivity was related to the distance between sites. Berumen *et al.* (2012) measured self-recruitment at a single, isolated island and connectivity between that island and two coastal sites located 25 and 33 km away for *Amphiprion percula* and *Chaetodon vagabundus*. They found that mean self-recruitment at the island was similar for both species and over 2 years, ranging between 40 and 65%. However, the strength of connectivity between the island and the two distant sites varied significantly between years for *A. percula* (connectivity for *C. vagabundus* was only measured in a single year). Finally, Saenz-Agudelo *et al.* (2012) conducted a 3-year study of a metapopulation of *A. polymnus* consisting of nine subpopulations spread over 35.5 km. They found that at both the level of the entire metapopulation and at the subpopulation level, self-recruitment was similar among years. However, unlike the two previous studies, they found that connectivity between subpopulations was broadly similar among years, and that the magnitude and temporal stability of connectivity between sites was related to the distance between sites. Overall, these temporal studies reinforce the assertion that self-recruitment is common in coral reef fish populations, while highlighting that connectivity between sites can be variable or consistent over time, perhaps as a result of species- or location-specific factors (Jones *et al.*, 2007; Pinsky *et al.*, 2012).

IV. IMPLICATIONS FOR CONSERVATION AND MANAGEMENT

(1) Implications for marine reserve network design

In the past decade, many papers and policy documents have put forth guidelines that have emphasised the need to incorporate ecological patterns of connectivity in marine reserve network design (e.g. Palumbi, 2004; Almany *et al.*, 2009; McCook *et al.*, 2009). However in this context, connectivity is often poorly defined, and guidelines that specifically address connectivity have focused on providing general guidance (e.g. take a system-wide approach that considers patterns and processes of connectivity within and among ecosystems: McCook *et al.*, 2009) or rules of thumb for size and spacing of marine reserves to protect most species (e.g. McLeod *et al.*, 2009).

Specific scientific advice regarding the configuration of marine reserves with respect to movement patterns of focal species can form an invaluable input to the MPA network design process, as demonstrated by the implementation of a state-wide network of MPAs in California that was informed by movement patterns of temperate species (Gleason *et al.*, 2013; Saarman *et al.*, 2013). Our synthesis of new information on the connectivity patterns of coral reef and coastal pelagic fishes allows us, for the first time, to provide specific advice on how to use connectivity to determine the size, spacing and location of marine reserves in tropical marine ecosystems, to maximise benefits for conservation and fisheries management of a range of taxa.

Marine reserves can be designed to provide protection for a broad array of species of interest (e.g. in a biodiversity conservation context) or a handful of important species (e.g. in a fishery management context) or a combination of both (Gaines *et al.*, 2010). Where the primary objective is to protect a few focal species, these guidelines can be specifically tailored to those species and their movement patterns. Where protecting multiple key species or a broad range of taxa is the focus, it may be necessary to identify a range of reserve sizes and spacing that maximises benefits across these taxa.

(*a*) *Size*

For marine reserves to protect biodiversity and enhance populations of fisheries species in fished areas, they must be able to sustain target species within their boundaries throughout their juvenile and adult life-history phases, when they are most vulnerable to fishing pressure (Palumbi, 2004; Hastings & Botsford, 2006; Gaines *et al.*, 2010). This will allow for the maintenance of spawning stock, by enabling individuals within reserves to grow to maturity, increase in biomass and reproductive potential, and contribute more to stock recruitment and regeneration (Russ, 2002).

Marine reserve size should therefore be determined by the rate of export of adults and juveniles (‘spillover’) to fished areas. Whilst spillover directly benefits adjacent fisheries, if the reserve is too small, excessive spillover may reduce fish density and biomass inside the reserve (Kramer & Chapman, 1999; Botsford *et al.*, 2003; Gaines *et al.*, 2010). This trade-off has led to divergent recommendations regarding the size of marine reserves for different objectives. From a conservation perspective, larger reserves (e.g. 10–20 km in diameter) are recommended because they enhance population persistence by increasing the protection of larger populations of more species (IUCN-WCPA, 2008; McLeod *et al.*, 2009; Gaines *et al.*, 2010; Saarman *et al.*, 2013). By contrast, smaller reserves (0.5–1 km across) have been recommended for fisheries management, since they protect some species and allow for the export of adults and larvae to fished areas, leading to direct benefits to fishers and potential increases in levels of recruitment (e.g. Alcala & Russ, 2006; Jones *et al.*, 2007; Harrison *et al.*, 2012).

Accordingly, marine reserve size should be informed by both management objectives and home range sizes of adults and juveniles of focal species (Table 1 and Fig. 1). Ideally, this information should be combined with knowledge of how individuals are distributed relative to one another (e.g. in exclusive *versus* overlapping ranges) to determine how many individuals a marine reserve of a specific size will protect. In the long term, this information might be accumulated through meta-analyses of fish densities from within well-designed and effectively implemented marine reserves, and models developed to refine recommended reserve sizes for species that take all aspects of their movement patterns into account.

Until such models are developed, we recommend that marine reserves should be more than twice the size of the home range of focal species for protection (in all directions, see Table 1). This will ensure that the reserve includes the entire home range of at least one individual, and will likely include many more where individuals have overlapping ranges (noting that a sufficiently large proportion of the meta-population must be protected overall: see Section IV.1*d*). For species that undergo ontogenetic shifts in habitat use, smaller marine reserves may be appropriate for nursery habitats if juveniles have smaller home ranges than adults (e.g. for some sharks: Speed *et al.*, 2010).

Some species (e.g. some groupers, surgeonfishes, grunts, snappers, goatfishes and parrotfishes) can be protected within small marine reserves (0.5–1 km across) because they do not move very far, while others are more wide-ranging (e.g. some jacks, sweetlips, groupers, wrasses, parrotfishes, snappers, emperors and sharks) and require medium to large marine reserves (2–5 or 10–20 km across, respectively: Table 1 and Fig. 1). Others move long distances and require very large marine reserves (20–100 km across or larger) such as some snappers, jacks, most sharks and manta rays. Since highly migratory pelagic fishes (e.g. tuna, billfishes and some mackerel) and oceanic sharks can range over much larger distances, marine reserves are likely to have limited utility for these species unless the reserves are thousands of kilometres across. Species that move over larger distances than a reserve size will only be afforded partial protection; however, reserves can provide benefits for these species if they protect specific locations where individuals aggregate and become especially vulnerable to fishing mortality (see Section IV.1*c*) (Norse *et al.*, 2005).

Optimal size will also depend on the level of resource use and the efficacy of other management tools. Where fishing pressure is high and there is no additional effective fisheries management in place outside reserves, then networks of both small and large marine reserves will be required to achieve both biodiversity and fisheries objectives. However, if additional effective management is in place outside reserves for wide-ranging species, then networks of small marine reserves can contribute to achieving both conservation and fisheries objectives (provided that a sufficiently large proportion of the meta-population is protected overall: see Section IV.1*d*).

A preliminary analysis of long-term monitoring of marine reserves in the Philippines suggests that using these recommendations for marine reserve size to protect focal species (Table 1) is likely to be successful. For example, species that do not move very far (e.g. the unicornfish *Naso vlamingii*, the surgeonfish *Ctenochaetus striatus* and small groupers such as *Cephalopholis argus* that move <0.1–0.3 km: Table 1) have shown significant increases in their density and abundance within small marine reserves such as Apo Island Marine Reserve (Russ *et al.*, 2004; Abesamis & Russ, 2005), which encompasses a 0.5 km long section of coral reef that is similar to the minimum marine reserve size recommended for those species (0.2–0.6 km: Table 1). Apo Island also demonstrates that small reserves can provide benefits for some wide-ranging species (e.g. the jack *Caranx sexfasciatus* that has core areas of use <3 km across), where they are combined with other fisheries management strategies (Maypa *et al.*, 2002; Maypa, 2012). By contrast, some species that move further and are more vulnerable to fishing (e.g. sharks that have core areas of use up to 10 km across such as *Carcharhinus melanopterus* and *Triaenodon obesus*) have not shown increases in their populations in this small reserve (A. White & R. Abesamis, personal observations). However, these shark species have shown a dramatic recovery in their density and biomass in the much larger Tubbataha Natural Park (A. White, unpublished data), which is a marine reserve that has a maximum reef length of 20 km that is large enough to protect these species. Sharks and jacks have also been found to be more abundant in larger *versus* smaller MPAs in others studies (e.g. in Hawaii: Friedlander, Brown & Monaco, 2007).

However, it is important to note that these recommendations regarding minimum reserve size based on movement patterns of focal species must apply to the habitats that adults and juveniles of these species use (rather than total size of the marine reserve *per se*). For example, if a reserve includes seagrass, coral reef and open water habitats, for species that use reef habitats only, the minimum size refers to the reef habitat that these species use within the reserve.

Larval dispersal also has implications for marine reserve size. For instance, Botsford, Hastings & Gaines (2001) recommended that reserves must be larger than the mean larval dispersal distance (at least twice the size) of the species they aim to protect in order for reserve populations to be self-sustaining. Since the best available empirical evidence indicates that coral reef fish larvae tend to settle on average 5–15 km from their parents (see Section III), reserves more than 10–30 km across are likely to be self-sustaining for these species. While smaller reserves are more likely to be sustained by connectivity with other populations rather than by self-seeding, the available empirical evidence also shows that self-recruitment at more limited spatial scales (<1 km) is common, indicating that a certain degree of larval retention usually occurs and that some larvae have limited dispersal. Thus, smaller reserves may still provide recruitment benefits within and close to their boundaries.

(*b*) *Spacing*

Benefits for both conservation and fisheries management are increased by placing reserves within a mutually replenishing network (McLeod *et al.*, 2009), with spacing such that reserves are highly connected to one another through larval dispersal (Shanks, Grantham & Carr, 2003; Palumbi, 2004; Almany *et al.*, 2009; Gaines *et al.*, 2010) while providing recruitment subsidies to fished areas (Botsford *et al.*, 2001, 2003, 2009*a*; Almany *et al.*, 2009). Data from the available empirical studies (Table 2) indicate that reef fish larvae tend to settle close to their parents and that linkages between local populations *via* larval dispersal are more likely to occur at limited distances (few tens of kilometers). Across species and locations, reef fish larvae appear to settle within 5–15 km of their parents on average; some larvae disperse up to 35 km from their parents, and a few larvae may disperse several hundred kilometres. At the same time, self-recruitment, even to small areas of habitat (diameters of 0.5–0.9 km), appears to be common and to occur consistently through time, indicating that short-distance dispersal is relatively frequent. This information is consistent with the prediction that the probability of successful larval settlement (and therefore the magnitude of recruitment) declines considerably with increasing distance from a source population (e.g. a reserve).

In terms of reserve spacing, the diminishing probability of successful larval dispersal with increasing distance from a source population (i.e. the shape of the dispersal kernel) may lead one to assume that situating reserves within a certain minimum distance from one another will provide sustaining recruitment (i.e. recruitment sufficient to equal or exceed natural mortality in a population; see Steneck *et al.*, 2009). However, there is no evidence to support this at present. At best, the available evidence suggests that larval connections between reserves are likely to be stronger at more limited spatial scales, e.g. <15 km.

Until better information is available, we recommend a maximum spacing distance between reserves of 15 km. This spacing distance is about 2–3 times greater than the typical larval dispersal distance estimated for several fishery and non-fishery species (Puebla *et al*., 2009; Pinsky *et al*., 2010; Harrison *et al*., 2012; Puebla, Bermingham & McMillan, 2012; Saenz-Agudelo *et al*., 2012) but conservative compared to the dispersal potential of other species (Table 2). Spacing reserves no more than 15 km apart will likely enhance the recruitment effect of reserves to other reserves and fished areas within that spatial scale. We further recommend that if reserves tend to be small as they are in certain regions (<1 km^2: see Section IV.1*d*), the spacing distance between them should be less than 15 km because the magnitude of larval export from the small source populations in these reserves will probably be less than from larger source populations in larger reserves.

Our recommendations with regards to spacing reserves may require revision as additional information from methods that can explicitly consider population persistence within reserve networks becomes available. However, it may be some time before information from such methods are available since they require empirical estimates of larval dispersal as well as information on population size, survival, and fecundity within patches (Burgess *et al*., 2014).

(*c*) *Location*

The location of marine reserves should largely be informed by information about the distribution of key habitats utilised by focal species and movement patterns of adults and juveniles among them (e.g. Olds *et al*., 2012). Since areas with high habitat connectivity can improve reserve performance (by supporting more species and maintaining ecosystem processes), these areas should be prioritised for protection (Edwards *et al*., 2010; Olds *et al*., 2012).

Furthermore, the location of a reserve to protect a particular species or group of species must be placed in the habitats that are suitable for the home ranges of those species. For example, marine reserves focused on protecting sharks should include coral reef habitats where reef sharks aggregate or show fidelity to specific sites (nursery, reproduction or feeding areas: see Section II.1), and extend a significant distance from the reef to incorporate deep-water foraging habitats of other shark species (e.g. *Carcharhinus albimarginiatus* and *Sphyrna lewini*: Hearn *et al*., 2010; Barnett *et al*., 2012).

To provide adequate protection for species that undergo ontogenetic habitat shifts, some portion of each habitat utilised by juveniles (e.g. recruitment hotspots: Wen *et al*., 2013) and adults should be protected within the same reserve. If multiple small reserves protecting different habitats are more feasible, they must be spaced to allow for movement among protected habitats.

For species that undertake spawning migrations, it is important to protect FSAs, migratory corridors and staging areas, in addition to protecting the home range of a sufficiently large proportion of their population (Rhodes & Tupper, 2008; Rhodes *et al*., 2012). If the temporal and spatial location of these critical areas is known, they should be protected in permanent or seasonal marine reserves (Zeller, 1998; Sadovy & Domeier, 2005; Rhodes & Tupper, 2008; Rhodes *et al*., 2012). If the location of these areas is not known, or if the scale of movement is too large to include in marine reserves (e.g. migration corridors), other management actions will be required (see Section IV.2).

Another consideration when placing reserves is maximising their potential to provide a source of larvae to other reserves and fished areas (Gaines *et al*., 2010). A common recommendation is to protect larval 'source' populations (e.g. Roberts *et al*., 2006; Almany *et al*., 2009), which can consistently provide larvae to other populations. In practice, identifying source populations is difficult and typically relies on oceanographic modelling (e.g. Bode, Bode & Armsworth, 2006). Furthermore, our review of larval dispersal studies indicates that delivery of larvae from one site to another is likely to vary in time, such that a location might act as a source in 1 year, but not another. Consequently, we recommend that marine reserves are located on the basis of key habitats and fish movements among these. However since currents are likely to influence dispersal to some degree, if there is a strong, consistent, unidirectional current, a greater number of marine reserves should be located upstream relative to fished areas.

Another aspect of larval dispersal that is relevant to selecting reserve sites is the need to protect spatially isolated populations (e.g. remote atolls). Isolated populations that are largely self-replenished have high conservation value, especially where they harbour endemic species and/or unique assemblages (Jones, Munday & Caley, 2002; Roberts *et al*., 2006). Low connectivity with other areas makes these locations less resilient to disturbance, so protecting a large fraction of their area may be required to ensure population persistence (Almany *et al*., 2009). Pinsky *et al*. (2012) suggest that populations or locations separated from their nearest neighbour by more than twice the standard deviation of larval dispersal would be largely reliant on self-recruitment for replenishment. In this context, and given the data so far obtained from dispersal studies, conservatively, a location or population >20–30 km from its nearest neighbour should be considered isolated and afforded greater protection.

(*d*) *Consideration of broader ecological and social factors*

The recommendations proposed above are based on larval dispersal and movement patterns (connectivity) alone. To inform real-world planning initiatives, these guidelines must be considered alongside other ecological criteria (Green *et al*., 2014), and applied within different, context-dependent, socioeconomic and governance constraints (Walmsley & White, 2003; Ban, Picard & Vincent, 2009; Lowry, White & Christie, 2009; Ban *et al*., 2011).

In addition to connectivity, there are other ecological considerations required to ensure that marine reserves are designed to maximise their benefits for conservation and fisheries management (reviewed in IUCN-WCPA, 2008; McLeod *et al.*, 2009; Green *et al.*, 2014). They include: representing 20–40% of each habitat in marine reserves (depending on fishing pressure, other fishery management measures, and the availability or rarity of habitats) to ensure that a sufficiently large proportion of the meta-population is protected overall; protecting at least three widely separated examples of each habitat in marine reserves (to minimise the risk that they might all be adversely impacted by a single disturbance); ensuring marine reserves are in place for the long term (preferably permanently); protecting special and unique areas in marine reserves (e.g. resilient sites, turtle nesting areas, FSAs); minimising and avoiding threats (such as land-based runoff) in marine reserves; and creating large multiple-use MPAs that include (but are not limited to) marine reserves. Whilst many of these guidelines can be applied alongside our recommendations regarding connectivity, some might create design trade-offs that need to be resolved. For example, small reserves should be spaced close together to maximise connectivity between them (see Section IV.1*b*), but this might require further replication of habitats in more distant reserves due to the increased likelihood of closely spaced reserves being impacted by a single disturbance event.

Social, economic and cultural factors often determine the degree to which ecological criteria regarding the optimal configuration of marine reserves can be applied (Ban *et al.*, 2009, 2011; Lowry *et al.*, 2009; Gleason *et al.*, 2013). For example in some situations, large marine reserves might be a viable option, e.g. in California (Gleason *et al.*, 2013) or in remote oceanic areas with small or no human populations (e.g. Tubbataha Reef, Philippines: Green *et al.*, 2011). However, in many countries with coral reefs, especially where communities rely heavily on these reefs for their livelihoods, large reserves are both socially and politically impractical (Ban *et al.*, 2011). In these settings, smaller reserves are more acceptable to local communities because they exclude smaller areas from fishing and fit within customary marine tenure boundaries or local government jurisdictions (Kramer & Chapman, 1999; Ban *et al.*, 2009). In these cases, reserves are commonly much smaller (∼1 km across: e.g. Weeks *et al.*, 2010) than typically recommended (e.g. 3–10 km across: Halpern & Warner, 2003; Shanks *et al.*, 2003).

Many previous recommendations for marine reserve design from a conservation perspective have conveyed the message that 'bigger is better' (e.g. Sale *et al.*, 2005; IUCN-WCPA, 2008; McLeod *et al.*, 2009). Whilst the results of this review reinforce this idea since larger reserves are able to provide protection for a broader range of species (Table 1, Fig. 1), they also demonstrate that smaller reserves can be effective for some species and objectives. For example, small reserves (e.g. 0.5–1 km long) are capable of providing protection for adults of fishery species that do not move very far (e.g. small groupers, parrotfishes, surgeonfishes and unicornfishes). Furthermore, self-recruitment seems highly probable even in small reserves. Thus small reserves should contribute to overall reserve network connectivity and persistence for some species provided that the reserves collectively represent a minimum proportion of the habitat of these species (20–40%) and they are close enough to each other to be connected by larval dispersal (Botsford *et al.*, 2001; Kaplan & Botsford, 2005). This conclusion is supported by empirical evidence that networks of small, well-designed and effectively managed marine reserves can provide local fisheries benefits for some species through adult spillover and larval export (e.g. Russ *et al.*, 2004; Harrison *et al.*, 2012; Almany *et al.*, 2013).

Nevertheless, for species with extensive movement patterns such as bumphead parrotfish, the minimum linear dimension of marine reserves would need to be at least 20 km (Table 1), which is much larger than the size typically implemented by coastal communities in many countries (most community-based marine reserves in Southeast Asia and the Pacific are <1 km across: e.g. Weeks *et al.*, 2010). Where marine reserves are smaller than the home ranges of species of interest, management strategies must be diversified to include alternative fisheries management tools designed to protect wide-ranging species outside reserves (see Section IV.2).

(2) Implications for other management strategies

Information regarding larval dispersal and movement patterns of populations of key species can also be used to inform other management strategies where marine reserves are either insufficient (e.g. for species that have large home ranges or undergo long-distance ontogenetic shifts or spawning or breeding migrations) or impracticable (e.g. where large marine reserves are not enforceable or favoured by communities). Alternative fisheries management strategies might include harvest controls such as catch, size, gear or effort restrictions, or outright bans on fishing for selected species or time periods to protect species with large home ranges or high vulnerability to fishing due to life-history characteristics (Hilborn *et al.*, 2006; Speed *et al.*, 2010; Sadovy de Mitcheson & Colin, 2012).

In many places, small marine reserves may be the only feasible spatial management tool (Alcala & Russ, 2006). However, in some contexts it may be possible to combine marine reserves with other spatial management tools to protect a broader range of species while also addressing socioeconomic and feasibility considerations. This may include combining marine reserves with adjacent limited-take or 'buffer' zones that provide additional protection for wide-ranging species that are unlikely to be protected within small marine reserves (e.g. humphead wrasse, bumphead parrotfishes and large grouper) or for all species except those that move over very large distances that are unlikely to benefit from marine reserves and are important for food security or economic reasons (e.g. tuna: see Gleason *et al.*, 2013; Saarman *et al.*, 2013). By combining these spatial management approaches, greater protection might be provided to more species over larger areas than could be achieved with marine reserves alone. For example in Palau, the protected area network is combined with legislation to protect wide-ranging species in a national shark sanctuary (www.sharksanctuary.com).

Coral reef species that move long distances to spawn (see Section II.2), are also likely to require a combined approach to management that protects their home ranges and spawning sites within reserves, and prohibits the capture and sale of reproductive adults during spawning migration and aggregation periods (Rhodes *et al.*, 2012) to prevent overfishing. Similar approaches might be required to protect species that undergo ontogenetic shifts in habitat use (i.e. seasonal fisheries restrictions during critical phases in their life history). Other management strategies may also be required to protect critical habitats, such as improved land use to protect coral reefs, mangroves and seagrass (Sanchirico & Mumby, 2009).

(3) Practical advice for practitioners

Of the suite of ecological criteria for marine reserve network design, connectivity has been one of the most challenging to put into practice (Almany *et al.*, 2009; McCook *et al.*, 2009), since empirical data for movement patterns of important species have typically been unavailable or inaccessible to those responsible for planning. Syntheses of available information for a broad array of taxonomic groups (combined with local knowledge) can help to overcome the problem of poor data availability in designing marine reserves for connectivity. However, a new challenge emerges in how to apply this information in different socioeconomic contexts.

The maximum size at which reserves are likely to be feasible (given socioeconomic constraints) may ultimately drive reserve design, but this should be informed by information regarding which species will or will not likely benefit from reserves, given their configuration (size, location, and distance from other reserves). In many contexts it will not be feasible, for example, to create marine reserves that are sufficiently large to protect the full range of species occurring within a region. However, having information on how different sizes of reserves may benefit different species provides a foundation for reserve design against which feasibility trade-offs can be explicitly evaluated. For example in a temperate context, information on adult movement patterns and larval dispersal distances informed easy-to-understand guidelines for size and spacing of marine reserves in a state-wide MPA network in California (Saarman *et al.*, 2013). The guidelines provided a framework that allowed participants to understand better which species might benefit from different sizes and spacing of MPAs, which informed a more realistic evaluation of trade-offs between protection and other socioeconomic considerations (Gleason *et al.*, 2013).

Information on species movement patterns can inform marine reserve network design in two ways – by identifying focal species for protection and determining the reserve configuration needed to protect them, or by using the configuration of proposed or existing reserves to evaluate which species might be protected within their boundaries (Fig. 2). Where reserve configurations are likely to be inadequate to protect focal species, their design should be refined or additional management tools will be required (see Section IV.2). This information can also be used to inform the design of programs to monitor the effectiveness of marine reserves by ensuring they focus on species likely to be protected by reserves with different configurations.

V. CONCLUSIONS

(1) Well-designed and appropriately managed marine reserves can be effective tools for biodiversity protection and fisheries management in tropical marine ecosystems. Benefits for both of these objectives can be increased by taking larval dispersal and movement patterns of focal species into account in marine reserve design.

(2) Marine reserves should be more than twice the size of the home range of adults and juveniles of focal species for protection (in all directions).

(3) Some species (e.g. some groupers, surgeonfishes, grunts, snappers, goatfishes and parrotfishes) can be protected within small marine reserves (<0.5–1 km across) because they do not move very far, while more wide-ranging species (e.g. some jacks, sweetlips, groupers, wrasses, parrotfishes, snappers, emperors and sharks) require medium to large (2–5 or 10–20 km across, respectively) or very large marine reserves (20–100 km across or larger). Marine reserves may have limited utility for highly migratory pelagic fishes (e.g. tuna, billfishes and sharks) that range over much larger distances unless the reserves are thousands of kilometres across.

(4) Optimal size will also depend on the level of resource use by people and the efficacy of other management tools: where fishing pressure is high and there is no additional effective fisheries management in place outside reserves, then networks of both small and large marine reserves will be required to achieve both biodiversity and fisheries objectives; if additional effective management is in place for wide-ranging species, then networks of small marine reserves can contribute to achieving both conservation and fisheries objectives (provided a sufficiently large proportion of the meta-population is protected overall).

(5) Marine reserves should include key habitats utilised by focal species (for home ranges, nursery grounds, migration corridors and spawning aggregations), and be located to accommodate movements among them.

(6) Species whose movement patterns are larger than a reserve size will only be afforded partial protection; however, reserves can provide benefits for these species if they protect specific locations where individuals aggregate and become especially vulnerable to fishing mortality (e.g. FSAs).

(7) Marine reserve benefits are increased by placing reserves within mutually replenishing networks with spacing such that reserves are connected to one another by larval dispersal of focal species, while providing recruitment subsidy to fished areas.

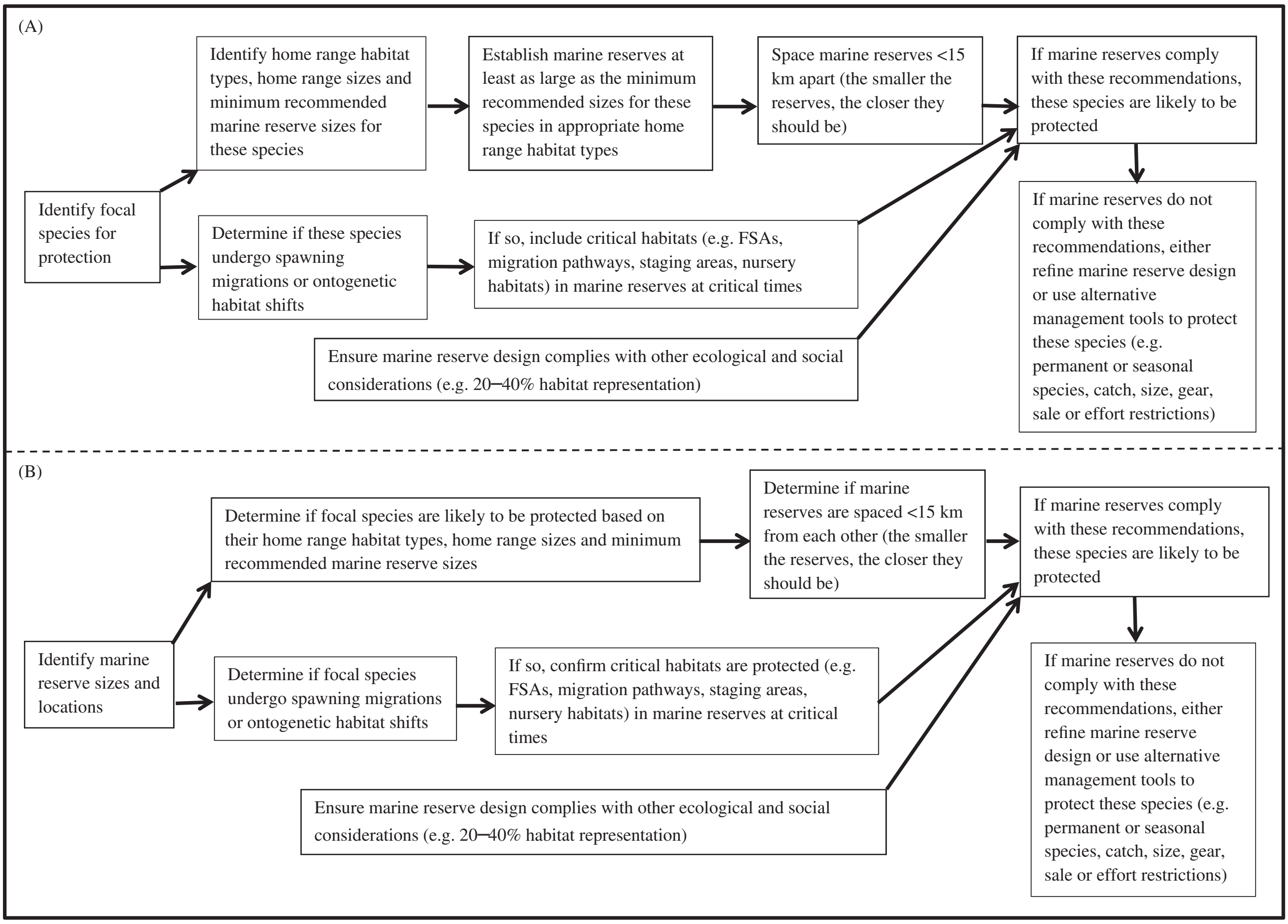

Fig. 2. Protocol for using connectivity information for marine reserve network design and adaptive management using either (A) focal species for protection or (B) marine reserve sizes and locations as starting points. Focal species may be high-priority species for fisheries, tourism or conservation (e.g. species listed as Vulnerable or Endangered on the IUCN Red List); home range habitat type is available in local fish identification guides and Fishbase (http://www.fishbase.org/); movement patterns (home range sizes, spawning migrations and ontogenetic habitat shifts) are summarized by taxa in Table 1 and Appendix S1, and by distance in Fig. 1; minimum recommended reserve sizes are provided in Table 1; and other ecological and social considerations are discussed in Section IV.1*d*. If a focal species is not listed in Table 1, Fig. 1 or Appendix S1, similar taxa might be appropriate proxies but caution should be taken when applying this approach. FSA, fish spawning area.

(8) Larval dispersal distances of coral reef fishes tend to be <5–15 km, and self-recruitment seems more common than previously thought, thus: reserve spacing should be <15 km with smaller reserves spaced closer together (although these recommendations may require revision as more information becomes available), isolated populations (>20–30 km from their nearest neighbour) should be afforded greater protection, and large marine reserves are more likely to be self-sustaining (although small reserves can provide recruitment benefits within and close to their boundaries).

(9) Larval sources are temporally variable and difficult to identify. So if there is a strong, consistent, unidirectional current, a greater number of marine reserves should be located upstream relative to fished areas.

(10) These recommendations can be used by practitioners to: design marine reserve networks to maximise benefits for focal species; review the configuration of existing marine reserves to ensure they are adequate to protect focal species; integrate marine reserves with other fisheries management tools; and refine monitoring programs to measure the effectiveness of marine reserves.

(11) These recommendations for marine reserve network design regarding connectivity of reef fish populations must be considered alongside other ecological design criteria, and applied within different, context-dependent, socioeconomic and governance constraints.

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VIII. SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article.

Appendix S1. Detailed summary of movement patterns reported for adult and juvenile coral reef and coastal pelagic fishes for a range of movement types, locations and habitat types based on a variety of methods and parameters.

Appendix S2. Methods used for adult and juvenile movement studies.

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