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PERSPECTIVE AND REVIEW

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# Larval ecology, dispersal, and the evolution of sociality in the sea

**Renata Mazzei** | **Dustin R. Rubenstein**

Department of Ecology, Evolution and Environmental Biology, Columbia University, New York, NY, USA

**Correspondence**
Renata Mazzei, Department of Ecology, Evolution and Environmental Biology, Columbia University, New York, NY 10027, USA.
Email: renata.mazzei@gmail.com

## Abstract

Individual decisions about whether or not to disperse shape the kin structure of social groups, promoting or disrupting the evolution of sociality via kin selection. It is often assumed that the great dispersal potential of marine larvae driven by ocean currents disrupts kin association and, as a consequence, reduces the chances that social groups in the sea form via kin selection. Yet, accumulating evidence indicates that the larval dispersal process is not as random as previously assumed and that different mechanisms can promote kin associations in marine species. Here, we review recent findings in the marine larval ecology literature, emphasizing key aspects of larval development that may limit or promote dispersal and the evolution of sociality in the sea. We find ample evidence that marine larvae settle closer to home than has been previously assumed. A variety of different mechanisms, including lack of planktonic dispersal, limited larval duration, larvae traveling together, variability in reproductive success, and behavioral and physical processes, can generate kin association in marine species and potentially lead to the formation of social groups via kin selection. Uncovering post-settlement dispersal patterns is also important for understanding how groups of unrelated individuals are formed. By integrating different larval dispersal strategies into the dual benefit framework for the evolution of sociality, we provide examples of alternative pathways for the evolution of sociality in marine species. Finally, we discuss how the increased use of parentage analysis in marine species will provide an opportunity for investigating whether kin selection is indeed much rarer in marine than terrestrial species. Ultimately, determining the role that dispersal and kin selection play in the evolution of sociality in marine species will require an increased effort to gather both behavioral and genetic data for the same species.

KEYWORDS
cooperation, dual benefits framework, group living, kinship, marine species, pelagic dispersal, social evolution

## 1 | INTRODUCTION

Dispersal, or lack there of, has long been thought to play a crucial role in the evolution of sociality because individual dispersal decisions shape the kin structure of social groups (Brown, 1974; Emlen, 1982, 1994; Hatchwell, 2009; Koenig, 1981; Koenig et al., 1992; Mumme, 1996). As related individuals accumulate in space, kin-selected benefits of helping relatives can promote the evolution of cooperative behaviors and sociality (Boomsma, 2009; Cornwallis et al., 2010; Hamilton, 1964; Lukas & Clutton-Brock, 2012). Yet, at the same time, social interactions among group members influence dispersal decisions, and the potential for competition among kin can favor dispersal (Hamilton, 1964; Queller, 1994; Smith, 1964; Taylor, 1992; West et al., 2002). Ultimately, the propensity to disperse therefore depends on the balance between the costs and benefits of dispersing versus remaining in the natal territory (philopatry). Although dispersal can reduce inbreeding risk or resource competition (Clobert et al., 2012; Johnson & Gaines, 1990), it may require greater energy expenditure and increase exposure to predation (Bélichon et al., 1996; Lucas et al., 1994). In contrast, by staying at home, individuals may inherit high-quality territories and breeding positions (Dickinson & Hatchwell, 2004). Since some direct benefits, such as territorial inheritance and dilution of predation risk, apply equally to related and unrelated individuals, direct rather than indirect benefits may drive the evolution of sociality when chances for kin interactions and indirect benefits are low, or when there is no cooperation over rearing young (Kingma et al., 2014; Stacey & Ligon, 1991). Thus, determining the costs and benefits of dispersal and philopatry is crucial to understanding the evolution of sociality, or the degree to which individuals tend to associate in social groups and form cooperative societies (Rubenstein & Abbot, 2017a).

Although marine species exhibit all of the forms of sociality described in terrestrial and freshwater animals—from pair living to eusociality (Hultgren et al., 2017; Taborsky & Wong, 2017)—they have been largely neglected in discussions of animal social evolution (Rubenstein & Abbot, 2017b). In terrestrial and some freshwater species, dispersal is typically an active process performed by juveniles or adults (Burgess et al., 2016). In marine species, however, dispersal is usually regarded as a passive process driven by ocean currents that disrupt kin association (Leis, 1991; Victor, 1984). As a consequence, dispersal in marine species has been considered less likely to lead to the formation of social groups via kin selection than it does in terrestrial species (Ruxton et al., 2014; Stiefel, 2013). However, evidence in a wide range of marine taxa suggests that larval dispersal is not as passive a process as previously assumed (Nanninga & Berumen, 2014). For example, larvae in many marine species have well-developed behavioral, sensorial, and navigational skills that allow them to change dispersal trajectories in combination with physical transport processes (Atema et al., 2002; Jeffs et al., 2009; Raimondi & Morse, 2000; Stobutzki & Bellwood, 1994; Vermeij et al., 2010; Wahab et al., 2011). It has also been recognized that long-distance dispersal can be costly and lead to phenotype–environment mismatches (Marshall et al., 2010). Indeed, marine species exhibit patterns of dispersal similar to terrestrial species, with a large number of offspring staying relatively close to home and only a smaller number of offspring dispersing longer distances (Almany et al., 2013; Buston et al., 2011; D'Aloia et al., 2013; Lowe & McPeek, 2014; Shaw et al., 2019). Furthermore, increasing evidence of kin association in marine species (e.g., Veliz et al., 2006; Selkoe et al., 2006; Bernardi et al., 2012; Iacchei et al., 2013; Selwyn et al., 2016; D'Aloia et al., 2018; Rueger et al., 2020; Robitzch et al., 2020) is challenging the view that dispersal of gametes and larvae is sufficient to prevent relatives from living together (D'Aloia & Neubert, 2018; Kamel & Grosberg, 2013). Finally, although most of the focus on dispersal in marine species has been on the planktonic larval phase, dispersal decisions are still important after settlement, particularly for group-living habitat specialists (Wong & Buston, 2013). Thus, understanding the costs and benefits of dispersal at different life-history stages, as well as their consequences for kin association and group living, can provide novel insights into how dispersal patterns affect the evolution of sociality in marine species with larval development.

Knowledge of larval dispersal patterns in marine environments has increased considerably in the past few decades, yet the link between dispersal patterns and sociality in marine species remains poorly understood. Here, we review the most recent findings in the marine larval ecology literature, focusing on key aspects of larval dispersal that may limit or promote the evolution of sociality in both marine vertebrates and invertebrates. First, we briefly summarize the main costs and benefits of pelagic dispersal, emphasizing the factors that might select for limited dispersal. Second, we examine recent findings on kin association in marine species and emerging hypotheses about pathways leading to the formation of kin structure in the sea. Third, we examine the factors influencing dispersal in the post-settlement phase and their consequences for social living among unrelated individuals. Finally, we review the recent methodological advances that have generated a better understanding of dispersal trajectories of marine larvae and discuss why these approaches will have important consequences for future studies of sociality in marine species. Ultimately, our goal is to synthesize emerging concepts and findings in the marine larval ecology literature that are slowly changing perceptions surrounding kin structure in marine populations, yet have thus far received little attention in the field of social evolution, particularly from researchers studying terrestrial organisms.

## 2 | COSTS AND BENEFITS OF PLANKTONIC DISPERSAL

The physical mediums of aquatic and terrestrial ecosystems impose different constraints and opportunities for organisms to disperse from where they were born. In the aquatic realm, water is an efficient medium for passive movement of small particles, while in the terrestrial environment, air is more efficient for active movement of larger-bodied organisms (Alexander, 2005; Dawson & Hamner, 2007; Hein et al., 2012). This is reflected in the fact that early life-history stages dispersing through air (e.g., seeds) have more adaptations for facilitating dispersal than early stages dispersing through water (e.g., gametes and larvae) (Burgess et al., 2016). In addition, planktonic suspension of larvae can reduce oxygenation constraints and provide food and protection from benthic planktivores, enabling larvae to feed, grow, and develop for days to months in the water without the need for parental care (Fernández et al., 2000; Strathmann, 1985). Finally, dispersal of small life-history stages should be more efficient in marine than freshwater environments because fewer absolute physical barriers in the sea reduce constraints to movement across large geographical distances.

Such increased efficiency of transportation and the potential benefits of evolving and maintaining a planktonic larval phase have led to the assumption that dispersal in marine species is often a by-product of traits selected for other functions (e.g., feeding, fecundity, predator avoidance), rather than a product of selection on dispersal itself (Bonhomme & Planes, 2000; Havenhand, 1995; Hedgecock, 1986; Johannes, 1978; Pechenik, 1999; Strathmann et al., 2002; Todd et al., 1998). However, planktonic dispersal also incurs costs, such as planktonic mortality or transport to unsuitable habitats (Pringle et al., 2014). Settling in unsuitable locations may be particularly costly when there are maternally-induced phenotypic adaptations to natal environments (Marshall, 2008) and the movement to distant locations leads to phenotype–environment mismatches (Marshall et al., 2010). In addition, for larvae that are not able to feed on plankton, long-distance dispersal may be energetically costly, leading to reduced effectiveness in habitat selection or physiological condition after colonization (Burgess et al., 2012; Marshall et al., 2010; Pechenik, 2006). Thus, it has been proposed that selection should limit, rather than favor, larval dispersal in marine species (Burgess et al., 2016). In fact, there is ample evidence that species with extensive potential for dispersal (e.g., with larvae that can survive for many weeks in the plankton) can limit dispersal with a variety of biophysical retention mechanisms. For example, larvae can alter their behavior (e.g., move vertically or horizontally) in conjunction with oceanographic phenomena such as tidal movements, which results in high rates of retention near natal reefs (Andutta et al., 2012; Cowen et al., 2003; Paris & Cowen, 2004; Sponaugle et al., 2002). Furthermore, a number of invertebrate species can produce two distinct types of larvae (a behavioral polymorphism called poecilogony) with different dispersal potential: pelagic feeding larvae versus benthic non-feeding larvae (Chia et al., 1996; Hoagland & Robertson, 2016; Levin & Todd, 1995). Such a variety of mechanisms for larval retention indicates that the costs of pelagic dispersal in marine species may actually be higher than previously assumed.

## 3 | LIMITED DISPERSAL AND PARENTAL CARE

Exploring the life-history traits of marine species that have limited larval dispersal may provide insights into the factors that select for dispersal retention, and ultimately to the evolution of sociality in the sea. Although most marine invertebrates and fishes have planktonic larval dispersal, some species entirely lack or limit pelagic dispersal by producing non-pelagic larvae (e.g., crawling larvae) or having brief larval durations (Jones, 2015; Shanks, 2009). Interestingly, the proportion of species with limited dispersal is higher in areas with cooler water temperatures and limited periods of high productivity, such as polar or deep-water ecosystems (Marshall et al., 2012). These conditions seem to restrict planktonic development, which requires warmer temperatures and higher food availability to minimize larval mortality due to advection (i.e., physical transportation of larvae to unsuitable habitats), predation, or starvation (Morges, 1995; Vance, 1973). There also seems to be an association between limited dispersal of marine invertebrates and the use of soft-bottom habitats (Grantham et al., 2003; Levin, 1984), where increased patchiness and disturbance rates may require rapid recolonization (Levin, 1984; Levin & Todd, 1995). Furthermore, in both marine invertebrates and reef fishes, limited dispersal seems to be associated with other reproductive and life-history traits such as increased egg size and parental care, as well as smaller adult body sizes (Barlow, 1981; Kasimatis & Riginos, 2016; Levitan, 2000; Strathmann & Strathmann, 1982). For example, limited dispersal is associated with viviparity in the black surfperch *Embiotoca jacksoni* (Froeschke et al., 2007) and with larger eggs, smaller adult size, and parental care in both the cardinalfish *Pterapogon kauderni* and the spiny damselfish *Acanthochromis polyacanthus* (Robertson, 1973; Vagelli, 1999).

The occurrence of both limited dispersal and parental care in the same species is particularly relevant because these life-history traits may provide a rare pathway for the evolution of sociality in the sea. In terrestrial species, parental care is an important precondition for the evolution of alloparental care, cooperative breeding, and eusociality, where individuals other than the parents provide care for the offspring (Jennions & Macdonald, 1994; Koenig & Dickinson, 2004; Wilson, 1975). Although extended parental care has evolved repeatedly in several species of crustaceans (summarized in Duffy & Thiel, 2007), direct parental care has never been documented in the only marine animal to exhibit eusociality, sponge-dwelling *Synalpheus* snapping shrimps (Dobkin, 1965; Duffy, 1996). However, the formation of family groups with multiple overlapping generations of offspring in *Synalpheus brooksi* (D. Rubenstein & J. Duffy, unpublished data) suggests that rudimentary parental care could exist in this group, despite the fact that observations of captive colonies have yet to reveal any evidence of direct care. In reef fishes, parental care is common in species with demersal eggs, but it is typically provided by only one parent, lasts for just a few days, and ceases at hatching, when the young ascend into the plankton (Almada & Santos, 1995; Barlow, 1981; Leis, 1991; Taborsky et al., 1987; Warner & Lejeune, 1985). However, in a few fish species with parental care and non-pelagic larvae, such as *A. polyacanthus* and three related species in the genus *Altrichthys*, both parents guard their brood for several weeks after hatching (Allen, 1999; Bernardi, 2011; Bernardi et al., 2017a, b; Kavanagh, 2000; Robertson, 1973). In addition, *A. polyacanthus* parents engage in energetically costly behaviors, such as aggressive offspring defense and partial feeding of offspring with mucus from their skin (Jordan et al., 2013; Kavanagh, 1998; Noakes, 1979; Robertson, 1973). Finally, the first evidence of conspecific alloparental care in coral reef fishes has only just been documented in *Altrichthys spp*., likely driven by adoption (Tariel et al., 2019). Although there is still no evidence of cooperative breeding in any coral reef fishes, marine species with non-pelagic larvae and biparental care seem promising systems for the evolution of sociality with potential cooperation among kin, deserving further investigation. Furthermore, parental care provided by only one parent might be sufficient for reducing or eliminating pelagic dispersal, increasing the chances of delayed dispersal and kin association.

## 4 | EVIDENCE AND MECHANISMS OF KIN STRUCTURE

With increasing recognition that marine species with a larval stage can limit or avoid pelagic dispersal, it is important to know whether limited dispersal translates into opportunities for kin association. A variety of different mechanisms have been proposed to explain the formation of kin structure in marine species with a larval stage (D'Aloia & Neubert, 2018). The most straightforward mechanism is by losing or delaying the pelagic stage altogether. In *Synalpheus* snapping shrimps, for example, eusocial and non-eusocial species differ by the absence of a pelagic phase in eusocial species. Although nearly all non-eusocial species of *Synalpheus* produce eggs that hatch directly into free-swimming larvae released into the water column, eusocial species produce eggs that hatch into non-swimming, crawling larvae that remain in the natal sponge (Dobkin, 1965; Duffy & Macdonald, 2010). As a consequence, eusocial species exhibit higher genetic relatedness within colonies than non-eusocial species (Duffy, 1996; D. Rubenstein & J. Duffy, unpublished data). Other marine colonial organisms with limited dispersal also show the potential for the formation of kin structure, whether inside an enclosed domicile or within a local area (i.e., the concept of kin neighborhoods, Hatchwell, 2009). For example, in the bryozoan *Bugula neritina*, larvae tend to settle nearby siblings and produce aggregations of closely related juveniles (Keough, 1984). In the ascidian *Botryllus schlosseri*, settling near-related and histocompatible individuals raise the chances of fusion and colony growth (Grosberg & Quinn, 1986). In marine fishes, small-scale spatial patterns of relatedness linked to non-pelagic larvae have been found in *E. jacksoni* (Bernardi, 2000), *P. kauderni* (Bernardi & Vagelli, 2004), and *A. polyacanthus* (Doherty et al., 1994; Planes & Doherty, 1997a, b; Planes et al., 2001). Finally, spatial genetic structure has also been found in the poecilogonic sea slug *Elysia pusilla*, indicating that low genetic divergence can also appear in species with intraspecific variation in larval development (Vendetti et al., 2012). However, not all species without a pelagic larval phase show the formation of local kin structure, as many species may still disperse through other mechanisms such as drifting, rafting, hitchhiking, creeping, or hopping (Winston, 2012). For example, some marine polychaete species living in vent ecosystems have evolved direct larval development, brood care, and/or parental care from broadcasting ancestors (Lucey et al., 2015), yet no evidence of kin structure in their colonies has been found thus far (Plouviez et al., 2008).

Evidence of high levels of self-recruitment (i.e., larvae returning to and settling in their natal population) has also been found for a number of marine invertebrates and vertebrates with a planktonic larval phase and extensive dispersal potential (Jones et al., 1999, 2005; Swearer et al., 1999; Almany et al., 2007, 2013; Christie et al., 2010; Hedgecock & Pudovkin, 2011; Saenz-Agudelo et al., 2012; Berumen et al., 2012; D'Aloia et al., 2013; Horne et al., 2016). Although self-recruitment does not necessarily lead to kin association, siblings and family groups have been found in the same reef, microhabitat, or sampling location in many studies (Barshis et al., 2011; Bernardi et al., 2012; Buston et al., 2009; D'Aloia et al., 2018; Dubé et al., 2020; Iacchei et al., 2013; Riquet et al., 2017; Rueger et al., 2020; Salles et al., 2016; Selkoe et al., 2006; Selwyn et al., 2016). In the hydrocoral *Millepora* cf. *platyphylla*, for example, sibship analysis showed that more than 40% of offspring settled less than 30 m from each other, resulting in sibling aggregations and spatial genetic structure (Dubé et al., 2020). In the cardinalfish *Sphaeramia nematoptera*, 3 out of 34 individuals that could be assigned parentage returned to the same social group and 8 to the same reef as their parents (Rueger et al., 2020). Similarly, in the three-spot damselfish *Dascyllus trimaculatus*, 11 groups of siblings (1 pair of full sibs and 10 pairs of half-sibs, out of 181 individuals) settled concurrently on a small reef (Bernardi et al., 2012). Finally, in the humbug damselfish *Dascyllus aruanus*, 35 pairs of close relatives were found within groups (out of the 265 individuals sampled, Buston et al., 2009). Different mechanisms have been shown to underlie these patterns of kin association, including siblings traveling and/or settling together (Bernardi et al., 2012; Knight-Jones, 1953; Robitzch et al., 2020), variability in reproductive success among individuals (Beldade et al., 2012; Christie et al., 2010; Hedgecock & Pudovkin, 2011), or physical transport processes (Barshis et al., 2011). Furthermore, it has been increasingly demonstrated that some marine larvae have extraordinary navigation skills, may respond to sensory cues (Atema et al., 2002; Gerlach et al., 2007; Kingsford et al., 2002; Leis, 2006; Montgomery et al., 2001), or have mechanisms of kin recognition (Grosberg & Quinn, 1986; Keough, 1984).

Ultimately, all of this evidence of kin association in marine species with different modes of larval dispersal may have important implications for the evolution of kin selection in marine species. Although the evolution of sociality with indiscriminate altruism is more likely in species that have completely lost a planktonic larval phase (e.g., *Synalpheus* shrimps), targeted cooperative behavior could still evolve partly by kin selection in species that show low within-group relatedness, but that can recognize, associate, and interact frequently with relatives (Buston et al., 2009). For example, in the emerald coral goby *Paragobiodon xanthosoma*, low but positive relatedness within groups has been suggested to explain why breeders tolerate subordinates (Rueger et al., 2021), while a combination of future selection and ecological/social constraints may explain why nonbreeders wait peacefully in a queue for breeding positions (Wong et al., 2007; Wong, 2010).

## 5 | POST-SETTLEMENT DISPERSAL PATTERNS

Post-settlement dispersal can also be relevant to the evolution of sociality in marine species. In some coral reef habitat specialist fishes, for example, philopatry can be explained by the benefits of inheriting a territory when there are limited chances to enter a new group and great risks of dispersing to obtain a new territory (Branconi et al., 2020; Wong, 2011). In the anemonefish *Amphiprion percula*, the goby *P. xanthosoma*, and the angelfish *Centropyge bicolor*, individuals form size-based dominance hierarchies in which subordinates queue for vacant breeding positions (Ang & Manica, 2010a; Buston, 2004b; Wong, 2010). Interestingly, dominant individuals in *A. percula* do not benefit from the presence of subordinates (Buston, 2004a), yet they tolerate them because subordinates maintain a safe size difference from dominants (Rueger et al., 2018). Likewise, *P. xanthosomus* and *C. bicolor* maintain strict size differences between dominants and subordinates (Ang & Manica, 2010a; Wong et al., 2007). Growth regulation by subordinates has been regarded as a cooperative act since it reduces the costs of conflict for dominant individuals (Bergmüller et al., 2007; Buston & Balshine, 2007; Huchard et al., 2016; Kokko et al., 2002), and therefore has been defined as peaceful cooperation (Buston, 2004a; Buston & Balshine, 2007). Yet, size differences among group-living fishes can be reinforced by the threat of punishment (Buston & Cant, 2006; Wong et al., 2007) or via direct aggression (Ang & Manica, 2010b). Cooperation among unrelated individuals also promotes group living in the yellow saddle goatfish *Parupeneus cyclostomus*, in which adults live either solitarily or in relatively stable groups formed of apparently unrelated individuals that cooperatively hunt mobile prey in corals (Strübin et al., 2011). Individuals have different hunting roles within a group and must signal when joining a new group, indicating that group membership must be negotiated (Strübin et al., 2011). Thus, dispersal and group integration in the post-settlement and even adult phase may play an important role in the evolution of sociality in marine species.

Another factor that influences post-settlement dispersal decisions and social grouping in marine species is the ability to change sex. In the polygynous gobiid fish *Trimma okinawae*, for example, females can change to males when becoming the largest individual in a social group, and change back to female if they change groups or if the group finds a larger breeding male (Sunobe & Nakazono, 1993). In some species of mollusks, growth and sex change are also influenced by interactions with conspecifics and local group composition (Collin et al., 2005; Warner et al., 1996; Wright, 1989), though it is unclear how often individuals change groups. Interestingly, some species of eusocial *Synalpheus* shrimps are also thought to be sequentially hermaphroditic, which may help reduce social conflict among females for access to breeding positions (Chak et al., 2015). The ability to change sex gives social marine species more flexibility to adjust to varying social conditions and introduces a uniquely sex-biased social structure that is not apparent in freshwater or terrestrial social species (Munday et al., 2006). Such an ability to change sex may be advantageous if the structure of social groups in the sea is more variable and less stable than those in freshwater and terrestrial environments.

## 6 | MARINE SOCIAL GROUPS AND THE DUAL BENEFIT FRAMEWORK

As exemplified in the dominance hierarchies of habitat specialist fishes, social group formation is not just based on the dispersal decisions of offspring and immigrants. Instead, current group members also have a say in whether they will allow "insiders" to remain in or "outsiders" to join the group. This conflict of interest has been previously recognized in terrestrial and freshwater social species (Giraldeau & Caraco, 1993, 2000; Higashi & Yamamura, 1993), and recently integrated into the dual benefit framework, which proposes that there are two distinct types of grouping benefits associated with sociality: resource defense and collective action benefits (Shen et al., 2017). Resource defense (RD) benefits derive from group-defended critical resources, whereas collective action (CA) benefits result from social cooperation among group members. Although this framework was originally proposed to explain the evolution of cooperative breeding, it may be useful for understanding how grouping benefits influence the evolution of sociality in marine species. For example, group living in marine invertebrates and fishes seems to be largely driven by RD benefits in habitat specialist species (Figure 1). That is, in *Synalpheus* shrimps, some damselfishes, and coral-dwelling gobies, individuals have strong habitat-specific requirements, but suitable habitats are limited (Branconi et al., 2020; Macdonald et al., 2006; Pratchett et al., 2012; Wong, 2010). To a lesser extent, CA benefits may be more critical for the formation of groups in the rarer cases of marine species that exhibit alloparental care (e.g., *Altrichthys* spp., Tariel et al., 2019) or cooperative hunting (e.g., *P. cyclostomus*, Strübin et al., 2011) (Figure 1).

Determining the primary grouping benefit for a species is important because insider–outsider conflict resolves differently in groups formed primarily because of RD or CA benefits (Shen et al., 2017). In cases where group formation is primarily driven by RD benefits, there are fewer reasons to accept outsiders, unless they are closely related and increase the per capita inclusive fitness of group members. In contrast, in cases where CA benefits are the primary driver of group formation, insiders should accept outsiders whether or not they are kin because increasing group size (up to an optimal number of individuals) should increase direct fitness gains of group members. This leads to the prediction that groups driven by CA benefits will be more variable in their genetic composition (but can still have some degree of within-group relatedness) and more frequently include non-kin than RD benefit-driven groups (Shen et al., 2017). Because relatedness data are unavailable for most marine species that live in social groups, we can only test these predictions in a few species where relatedness is known or by inferring relatedness levels from the dispersal strategy used by the species (Figure 1). As predicted, RD benefits in the habitat specialist *Synalpheus* shrimps and *Dascyllus* damselfishes are linked to a lack of planktonic dispersal and larvae traveling together, respectively, both of which facilitate the accumulation of kin leading to high and intermediate levels of relatedness among group members (Chak et al., 2017; Tariel et al., 2019). In contrast, limited dispersal and high or intermediate relatedness seem to be connected with CA benefits in *Altrichthys* fishes, whereas broadcast dispersal and low relatedness seem to be connected with RD benefits in the habitat specialists *A. percula* and *P. xanthosomus*, but CA benefits in the cooperative hunter *P. cyclostomus*.

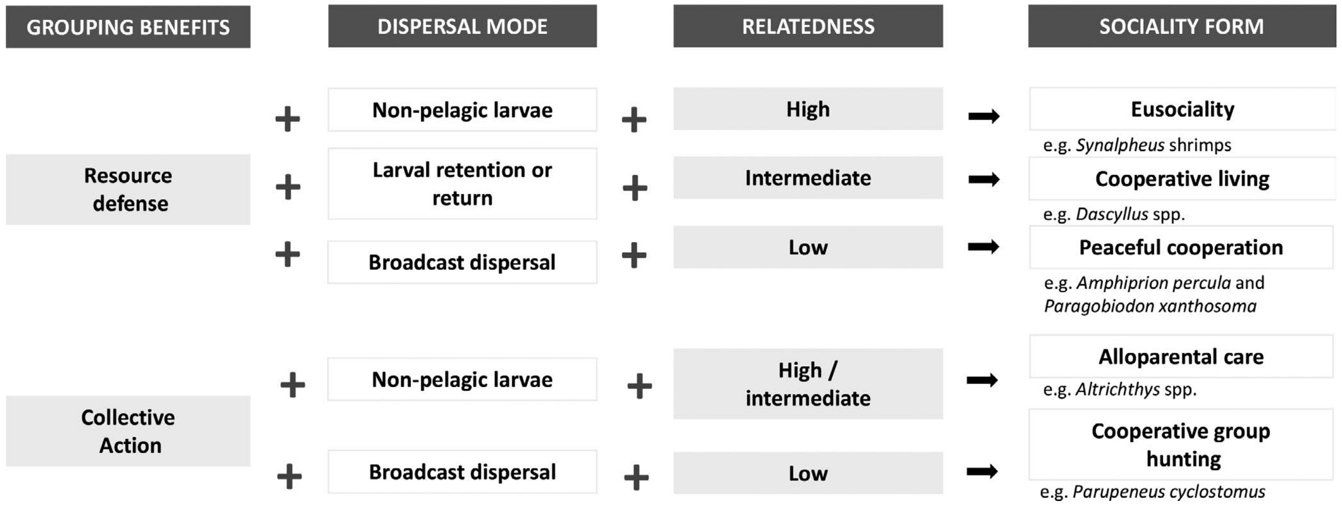

FIGURE 1 Examples of potential pathways for the evolution of sociality in marine species by integrating the dual benefit framework (Shen et al., 2017) with marine dispersal strategies and levels of within-group relatedness. Resource defense (RD) benefits derive from group-defended critical resources, whereas collective action (CA) benefits result from social cooperation among group members. Although the dual benefit framework generally predicts that groups driven by CA benefits will show lower within-group relatedness than groups driven by RD benefit, marine species that form social groups may have the potential to show alternative links between grouping benefits and relatedness compared with terrestrial species. We have only depicted pathways with known examples, but other starting points, pathways, and links between sociality and dispersal mode might be equally possible in marine species

Interestingly, the peaceful cooperation among unrelated group members in marine habitat specialists seems to be an exception to the RD benefit hypothesis, which predicts that only related outsiders will be accepted when there is high habitat saturation (Shen et al., 2017). In this case of peaceful cooperation, tolerance of unrelated outsiders is controlled by the regulation of strict size-based dominance hierarchies (Branconi et al., 2020). This might be relatively easier for marine species with larval development, because outsiders join the group when they are very small (settling larvae), which may facilitate their adjustment to the size-based dominance hierarchy during early development. In contrast, terrestrial and freshwater social species typically migrate as juveniles or adults, and acceptance into a new group can be a lengthy and complex process that requires repeated prospective visits (Jungwirth et al., 2015). Thus, although the predominance of a larval stage in marine species is often seen as a barrier to the evolution of cooperative group living driven by kin selection, it might actually be an advantage in the evolution of peaceful cooperation. Furthermore, recent evidence suggests that low but positive relatedness might have a small role in explaining peaceful cooperation in *P. xanthosomus* (Rueger et al., 2021), which highlights the importance of measuring genetic relatedness in marine social groups for betting understanding their grouping benefits. Ultimately, the dual benefit framework may prove useful for not only testing the grouping benefits hypotheses in the few social marine species studied thus far, but also predicting which types of species might form social groups and therefore warrant further study. Likewise, studies using genetic approaches to understand larval dispersal patterns may serve as a road map for identifying marine species with higher levels of kin association and group relatedness.

## 7 | APPROACHES FOR DESCRIBING LARVAL DISPERSAL PATTERNS AND RELATEDNESS

Although the idea of tracking the movement of tiny larvae in the immensity of the ocean was once considered to be impossible, our understanding of marine larval dispersal has greatly advanced in the past few decades as new tools and techniques have become available to track animal movements in the sea (Jones, 2015; Levin, 2006). With the accumulation of new data, marine ecologists have altered their view that marine populations are predominantly "open," or connected by larval dispersal over long distances, to one where a higher proportion of larvae settle closer to home than was previously realized (Jones, 2015; Levin, 2006). Initial attempts to address larval connectivity focused on understanding marine population dynamics and their consequences for the management of fisheries stocks (Botsford et al., 2001; Cowen, 2002; Lubchenco et al., 2003). Using this approach, it became evident that a good understanding of larval connectivity was crucial for efficiently designing marine protected areas (Cvitanovic et al., 2013; Jones et al., 2007; Sale et al., 2005), predicting the spread of invasive species (Fletcher et al., 2013; Luiz et al., 2013; Puth & Post, 2005), and determining how populations of organisms respond to climate change (Travis et al., 2013).

More recently, a variety of approaches have been used to estimate dispersal of marine organisms at different ecological scales (reviewed in Jones, 2015; Levin, 2006). Population genetics, otolith chemistry, and biophysical models are efficient methods for describing larger-scale population subdivisions (Planes, 2002), as well as estimating dispersal distance (Kinlan & Gaines, 2003; Palumbi, 2003) and direction (Herwerden et al., 2009). Although these methods have been used to predict natal origins or dispersal pathways of larvae, only two methods can directly link individual juveniles to their spawning locations: larval tagging and genetic parentage analysis. Larval tagging can be achieved by marking demersal eggs or injecting ripe females with chemical substances or trace elements that are transferred to the larvae (DiBacco & Levin, 2000; Elsdon et al., 2008; Thorrold et al., 2011). Since both tagging methods require great mark and recapture effort and can be expensive, their application has been limited thus far (Jones, 2015). In contrast, with the rapid development of next-generation DNA sequencing techniques, genetic parentage analysis has become increasingly popular and proven a successful method for describing patterns of larval dispersal, particularly for small reef fishes (Harrison et al., 2013; Jones et al., 2005; Planes et al., 2009). This method assigns individual juveniles to one or both parents and can be used to examine genetic relatedness among individuals in larval cohorts and social groups. By providing increasing evidence of kin association in marine species with pelagic larval dispersal (Barshis et al., 2011; Bernardi et al., 2012; Buston et al., 2009; Iacchei et al., 2013; Riquet et al., 2017; Selwyn et al., 2016), the use of parentage analyses has challenged the predominant assumption that pelagic dispersal disrupts kin structure in marine species (D'Aloia & Neubert, 2018; Kamel & Grosberg, 2013).

Ultimately, determining the role that dispersal and kin selection play in the evolution of sociality in marine species will require both behavioral data and genetic data for the same species. For example, researchers need to know whether species that associate with kin exhibit social behaviors such as joint territorial defense, group living, or even cooperative breeding or eusociality. At the same time, relatedness data are missing for most species of demersal spawners that exhibit different forms of parental care. Only by filling these critical knowledge gaps—something that can be done with molecular tools—will we be able to determine how different dispersal and life-history strategies may lead to the evolution of sociality in the sea.

## 8 | CONCLUSIONS AND FUTURE DIRECTIONS

Growing evidence on the potential of larval retention and kin formation in marine species is altering the perception that kin selection theory has a limited role in the evolution of sociality in marine species. The marine larval ecology literature has shifted its predominant view that marine species are well-connected via long-distance dispersal to include more structured population models of larval dispersal. Now, it is largely recognized that marine larvae settle closer to home than was once realized, and empirical and theoretical results suggest that kin cohesion and/or limited dispersal may lead to kin association. Thus, the role of kin selection in the formation of marine social groups should not be ruled out from the start. The dual benefit framework (Shen et al., 2017) provides a predictive theoretical framework that may be particularly useful for studying social evolution in the marine environment because it considers different types of potential reproductive benefits associated with group living, as well as how dispersal, environmental constraints, and insider–outsider conflict influence grouping. Moreover, the framework can be used to make predictions about which types of species may form groups of kin versus non-kin, as well as which types of species might warrant further study of their social behavior and organization. While the lack of pelagic larvae may facilitate the formation of family groups and the evolution of altruistic social behaviors, larvae with limited dispersal and/or the ability to return to natal reefs may also facilitate kin interaction and association, and ultimately the evolution of cooperative behaviors. Moreover, dispersal decisions in the post-settlement phase seem to play an underappreciated role in the evolution of "peaceful cooperation" in coral reef habitat specialists, a promising system for the study of sociality in groups of mostly unrelated individuals. With the advance and increased use of larval tracking and parentage analysis in marine populations, a growing list of systems with the potential to form cooperative groups will be readily available to behavioral ecologists and evolutionary biologists interested in the evolution of sociality in the sea.

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## CONFLICT OF INTEREST

The authors have no conflicts of interest to declare.

## ETHICAL APPROVAL

No approval of research ethics committees was required to accomplish the goals of this study because no data were generated for this paper.

## ORCID

*Renata Mazzei* https://orcid.org/0000-0001-5370-4528
*Dustin R. Rubenstein* https://orcid.org/0000-0002-4999-3723

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