

LARVAL SETTLEMENT IN ECHINODERMS: A REVIEW OF PROCESSES AND PATTERNS

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Abstract Echinoderms are a common component of benthic marine ecosystems, with many being ecologically and/or economically important. Like many marine organisms, most echinoderms have a bipartite life history with a planktonic larval phase and a benthic adult phase. The transition between these phases (i.e. settlement) is complex and comprises a cascade of events including the location, exploration and selection of suitable benthic habitat, and metamorphosis to adapt from a pelagic to a benthic lifestyle. This review provides a comprehensive synthesis of the various processes involved in the settlement phase across all five extant classes of echinoderms. Central to the review is a detailed assessment of settlement behaviour and the diverse mechanisms of settlement induction. Most echinoderms, including keystone sea urchins, starfishes and sea cucumbers, do not settle indiscriminately; specific environmental conditions or cues are often necessary for settlement to occur, resulting in marked spatial and temporal variability in settlement rates. Fluctuations in settlement, in turn, lead to major changes in the local abundance of echinoderms and often have profound ecological consequences, due to the pivotal role that many echinoderms play in ecosystem functioning. Given important knowledge gaps persist, this review also explores opportunities for future research to advance our understanding of this critical early life-history phase.

Keywords: Marine Ecology; Environmental Cues; Settlement Induction; Larval Behaviour; Metamorphosis; Recruitment; Marine Benthic Invertebrates

Introduction

Echinoderms (phylum Echinodermata) are commonly observed across all benthic marine habitats, ranging from exposed rocky shores and tropical coral reefs to the sandy floor of deep-sea habitats (Byrne 1990, Keesing et al. 1993, Sumida et al. 2000). There are approximately 7000 extant species (Pawson 2007) across five classes (Byrne & O'Hara 2017): Echinoidea (sea urchins, sand dollars and heart urchins), Asteroidea (starfishes or seastars and sea daisies), Ophiuroidea (brittle stars, basket stars and snake stars), Holothuroidea (sea cucumbers) and Crinoidea (feather stars and sea lilies). Echinoderms are economically important with extensive commercial fisheries for sea cucumbers (Holothuroidea) and sea urchins (Echinoidea), which are increasingly supplemented by aquaculture (Brown & Eddy 2015). Echinoderms are also ecologically important. Sea cucumbers, for example, make important contributions to nutrient cycling and energy transfer (Purcell et al. 2016). Other

echinoderms have been shown to be important ecosystem engineers (Lessios et al. 1984, Carpenter 1985) and/or keystone species (Paine 1969, Hughes et al. 1985, Ling et al. 2015, Byrne et al. 2016, Menge et al. 2016).

Large fluctuations in population density are a salient characteristic of many echinoderms (Uthicke et al. 2009) and can have important consequences for ecosystem structure and function (Chesher 1969, Birkeland 1989, Estes et al. 2011, Ling et al. 2015). For example, the proliferation of sea urchins and subsequent overgrazing in many temperate reef systems has contributed to loss of kelp forest and macroalgal beds (Ling et al. 2015). Conversely, population collapse in keystone predator starfish species across the Northeast Pacific (Menge et al. 2016, Schultz et al. 2016, Harvell et al. 2019, Kay et al. 2019) has triggered trophic cascades and changed shallow water seascapes. On tropical reefs in the Caribbean, population collapse of the sea urchin *Diadema* contributed to shifts from coral- to algal-dominated habitats (Lessios et al. 1984, Carpenter 1985, Hughes et al. 1985). Periodic population eruptions of coral-feeding crown-of-thorns starfishes (*Acanthaster* spp.) have also been a major contributor to sustained coral loss and reef degradation on many Indo-Pacific reefs (Bruno & Selig 2007, Kayal et al. 2012, Mellin et al. 2019). Ecological studies of echinoderms are, therefore, often focused on understanding causes of population fluctuations (Ling et al. 2019, Glockner-Fagetti & Phillips 2020, Caballes et al. 2021), which are inextricably linked to life-history processes that affect larval ecology and patterns of settlement or recruitment (e.g. Ebert 1983, Uthicke et al. 2009, Metaxas 2013).

Echinoderms exhibit considerable life-history diversity (Byrne et al. 1999, McEdward & Miner 2001, 2007, Byrne & O'Hara 2017, Ebert 2021a), but are generally gonochoric, and reproduce sexually by broadcast-spawning gametes that are fertilised externally. Accordingly, most echinoderms have a planktonic larval phase, which lasts from days to months (Strathmann 1987, Hadfield et al. 2001). Larval development is characterised by a series of distinct developmental stages (Byrne 2013, Byrne & O'Hara 2017). Many echinoderms have lecithotrophic larvae (McEdward & Miner 2001, 2007, Uthicke et al. 2009), meaning that they do not or cannot feed, and larval duration is constrained by initial energy reserves. Most of the best known and extensively studied echinoderm species (e.g. *Acanthaster* spp., *Diadema* spp.) are, however, planktotrophic (Uthicke et al. 2009), and this capacity to feed means that larvae may remain in the plankton for much longer (*cf.* lecithotrophic larvae) and potentially disperse much further (Emler 1995). More importantly, egg size and energy content (= maternal provisioning) are significantly higher in species with lecithotrophic larvae (McEdward & Chia 1991, Falkner et al. 2015), which consequently constrains fecundity. Echinoderms with planktotrophic larvae have potentially much higher reproductive capacity (Uthicke et al. 2009), but the extent to which the reproductive capacity is realised depends on exogenous food availability for larvae.

Despite the wide range of biotic (e.g. predation and starvation) and abiotic factors (e.g. dispersal to unfavourable habitats) that may constrain larval development and survival (Rumrill 1990, Lamare & Barker 1999, Cowan et al. 2016a, 2020), population replenishment and dynamics of echinoderms (like all marine species with a dispersive larval phase) is also conditional on settlement success and early post-settlement survival (Balch and Scheibling 2001). After completing larval development, echinoderms undergo metamorphosis, wherein they rapidly develop morphologies that are adapted to their benthic adult habit (*sensu* Hadfield et al. 2001). This planktonic-benthic transition, hereafter referred to as settlement (*sensu* Scheltema 1974), comprises a cascade of events that often occur rapidly, but can have far-reaching consequences for the population dynamics and distribution of echinoderms, and the ecosystems in which they play important roles. To assess these potential consequences, a comprehensive understanding of the environmental conditions and cues necessary for echinoderm larvae to settle, and how they translate to concomitant settlement patterns in the field is needed.

Past reviews of settlement induction and metamorphosis in marine invertebrate larvae have largely focused on ascidians, cnidarians, corals, hydroids, molluscs and/or polychaetes (e.g. Burke 1983a, 1986, Pawlik 1992, Rodríguez et al. 1993, Wiczorek & Todd 1998, Hadfield & Paul 2001, Hadfield 2011). Despite extensive primary research on settlement in echinoderms (e.g. Birkeland et al. 1971, Cameron & Hinegardner 1974, Highsmith 1982), there has been limited synthesis or review of this work. Strathmann (1978) and Pearce (1997) reviewed settlement induction in echinoderm larvae. Meanwhile, Balch & Scheibling (2001) provided a comprehensive synthesis of patterns of echinoderm recruitment, building on the initial review of recruitment patterns by Ebert (1983). General patterns of settlement are also briefly summarised in more recent syntheses focusing on the larval ecology of echinoids (Metaxas 2020) and asteroids (Metaxas 2013). However, a considerable body of research from the past two decades has substantially advanced our understanding of the processes and patterns of settlement in echinoderms. It is therefore timely to provide a comprehensive, phylum-wide review covering all aspects of this critical and complex early life-history phase.

The aim of this review is to synthesise foundational research and recent advances in the study of the various processes and patterns in echinoderm settlement. Importantly, our review provides a detailed overview of published work on larval settlement across a wide range of marine habitats and environments. We start with a summary of the complex mechanisms and processes taking place during this planktonic-benthic transition. Central to our review is a detailed synthesis of settlement behaviour and the various mechanisms of settlement induction, including both natural and artificial chemical cues. We then critically assess predominant sampling techniques used to measure settlement *in situ*, followed by a review of spatial and temporal settlement patterns, which allows for comparisons among echinoderm classes and species across various marine habitats, locations and climate zones. The final section of this review highlights persistent and critical information gaps and outlines future directions for research pertaining to this important early life-history phase.

Larval settlement: the planktonic-benthic transition

Terminology

While often used interchangeably to describe planktonic-benthic transitions, settlement and metamorphosis are distinct processes for echinoderms. Scheltema (1974) defined settlement as a behavioural response of planktonic larvae resulting in the termination of their pelagic larval stage and assumption of a benthic life. As such, settlement typically refers to the descent from the water column and contact with the substratum. However, such substratum contact is reversible (Burke 1983a, Crisp 1984, Pawlik 1992, Hadfield & Paul 2001), whereby larvae may abort their benthic habit and resume swimming to seek out alternative settlement substrates or habitats (Figure 1). By contrast, metamorphosis is considered an irreversible morphogenic event, which includes the loss of larva-specific and emergence of juvenile-specific structures (Figures 2 and 3, Hadfield & Paul 2001). Moreover, metamorphosis may occur before or after the contact with the substratum, depending on the species (Figure 1).

For the purpose of this review, settlement will be used to refer to the more general definition of the transition from the planktonic larval to the benthic, post-metamorphic stage, as used in many other marine taxa (Hadfield 1986, Pawlik 1992, Rodríguez et al. 1993). In many echinoderms, this settlement phase may include various behavioural components (*sensu* Crisp 1984). We only use the morphogenic term ‘metamorphosis’ in specific reference to the physiological and morphological changes involved in this event, which appears necessary given some echinoderms metamorphose in

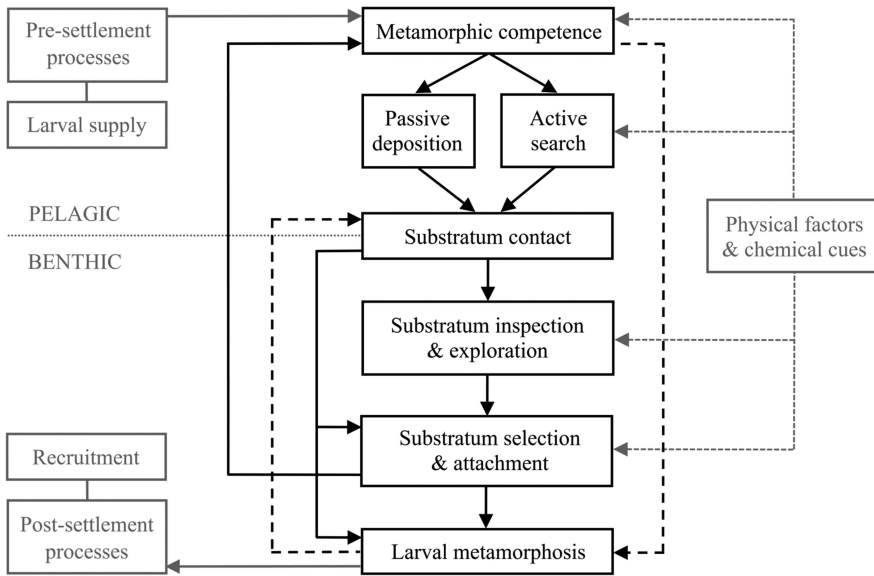


Figure 1 Key stages and processes in the settlement of echinoderms with planktonic larvae. Some echinoderms metamorphose in the plankton prior to contacting the substratum (dashed black arrows).

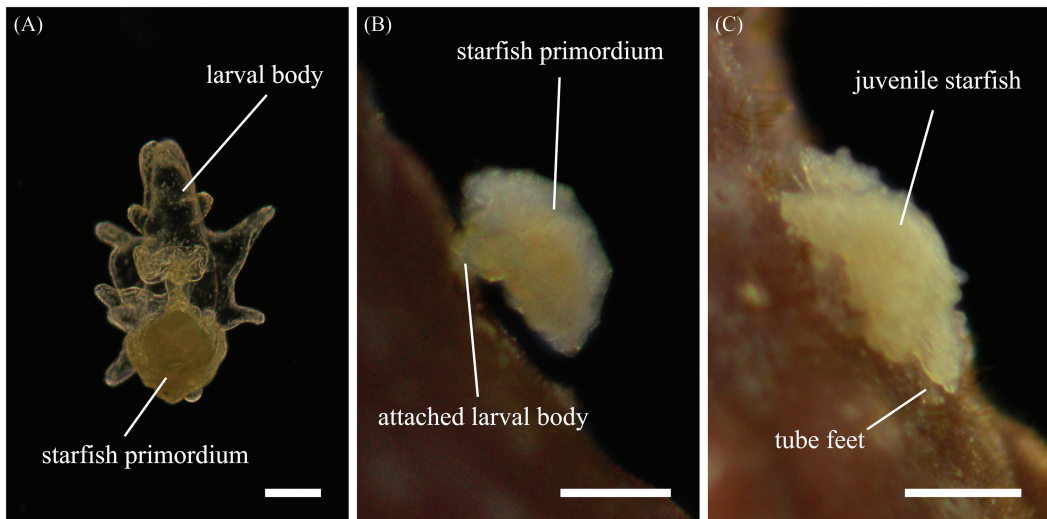


Figure 2 Larval development through metamorphosis in the Pacific crown-of-thorns starfish (*Acanthaster cf. solaris*), an ecologically important asteroid with a pelagic planktotrophic larval stage and complex larval morphogenesis: (A) brachiolaria larva; (B) metamorphosing larva absorbing the larval body; (C) post-metamorphic juvenile. Scale=0.25 mm. Photographs by C.F. Caballes.

the plankton prior to contacting any substratum (Domanski 1984, Hendler 1991, McEdward & Miner 2001, Selvakumaraswamy & Byrne 2004), and numerous studies specifically report metamorphic responses of echinoderm larvae (e.g. Pearce & Scheibling 1991, Yazaki & Harashima 1994, Naidenko 1996, Matsuura et al. 2009).

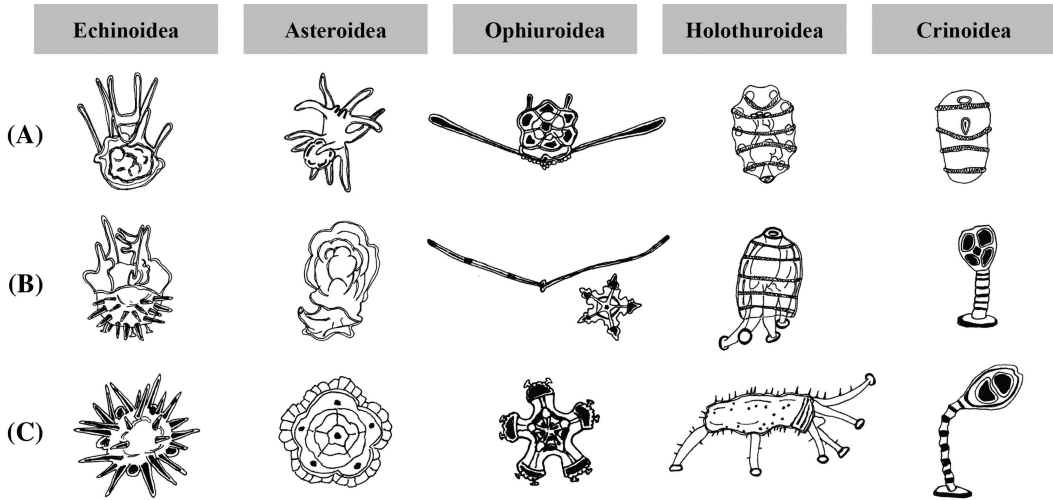


Figure 3 Echinoderm larval development through metamorphosis, as exemplified by an echinoid (*Tripneustes gratilla*), asteroid (*Acanthaster cf. solaris*), ophiuroid (*Ophiothrix exigua*), holothuroid (*Holothuria scabra*) and crinoid (*Antedon serrata*): (A) late-stage larva; (B) settlement and metamorphosis; (C) post-metamorphic juvenile. Illustrations by C.F. Caballes; based on Caballes & Pratchett (2014), Kitazawa et al. (2015), Toha et al. (2017), Yamakawa et al. (2020) and Nontunha et al. (2021).

Pre-settlement processes

A range of abiotic and biotic factors may influence echinoderm larvae prior to settlement. Crucially, mortality is thought to be very high during the sometimes highly prolonged planktonic larval stage (Cameron et al. 1985, Bosch et al. 1987, Pratchett et al. 2017, Ebert 2021b). With a few exceptions (Rumrill 1987, López et al. 1998, Lamare & Barker 1999), most estimates of larval mortality in echinoderms come from controlled laboratory studies, such that larval mortality may be even higher in natural environments, due to increased environmental fluctuations, limited prey availability and potentially high rates of predation (Pearse & Cameron 1991, Ebert 2021b).

The principal abiotic (environmental) factors affecting echinoderm larvae during their planktonic life stage are thought to be advection, temperature and salinity (reviewed by Balch & Scheibling 2001). Most notably, the dispersal and distribution of planktonic larvae depends on advective transport, which in turn is driven by large-scale oceanographic features and currents, and local hydrodynamics (Ebert 1983, Pearse & Cameron 1991). Given their generally limited swimming capacity, larval dispersal models often assume that echinoderm larvae are passive particles (Montgomery et al. 2017), although swimming is critical in determining larval distribution and settlement patterns at relatively small spatial scales. The important role of hydrodynamic forces in determining large-scale (e.g. inter-reef) patterns of species' distributions and population connectivity has been demonstrated for the Pacific crown-of-thorns starfish *Acanthaster cf. solaris* (Black & Moran 1991; Hock et al. 2014) and the echinoid *Centrostephanus rodgersii* (Banks et al. 2007). However, detailed biophysical models which incorporate species-specific knowledge of larval biology and behaviour (e.g. Bode et al. 2019) are yet to be developed for any echinoderm species.

Changes in key physical variables such as temperature and salinity may also influence larval development (Byrne et al. 2009, Li et al. 2011a, Privitera et al. 2011, Kamyra et al. 2014), survival (Lucas 1973) and planktonic larval duration (Thorson 1950, Agatsuma et al. 1998). For example, larvae of the echinoid *Dendraster excentricus* take three times as long to reach the six-armed larval stage at 12°C compared to 22°C (McEdward 1984). Numerous studies attribute fluctuations in

reproductive behaviour and settlement rates of echinoderms to changes in temperature (Balch et al. 1999, Hernández et al. 2010, Sotelo-Casas et al. 2016, Glockner-Fagetti & Phillips 2020, Okamoto et al. 2020, Caballes et al. 2021), although these patterns may be conflated by simultaneous changes in a range of environmental conditions. In some echinoids, temperature changes have explicitly been linked to population irruptions and range extensions (Hart & Scheibling 1988, Ling et al. 2008, 2009).

In terms of biotic factors, predation and starvation in the pelagic developmental habitat have long been recognised as key factors contributing to high levels of mortality among planktotrophic larvae across a range of marine taxa (Thorson 1950, Birkeland 1982, Young & Chia 1987). For echinoderms, laboratory experiments have demonstrated the importance of predators in regulating larval densities (Rumrill & Chia 1985, Cowan et al. 2016a, 2020). At the same time, food availability and potential starvation inherently constrain the condition, size and survival of planktotrophic echinoderm larvae that are reliant on exogenous nutrition to complete development and facilitate settlement (Basch & Pearse 1995). Larval starvation has been viewed as less important than predation in directly limiting larval supply (Pearse & Cameron 1991); however, for several echinoderm species, there is experimental evidence that larval nutrition influences the quality and quantity of planktotrophic larvae (Fenaux et al. 1994, Fabricius et al. 2010). Spatiotemporal variation in settlement rates of echinoderms has been attributed to differences in phytoplankton availability in the weeks or months preceding settlement (Hernández et al. 2010, García-Sanz et al. 2014, Glockner-Fagetti & Phillips 2020, Okamoto et al. 2020), suggesting that food availability may exert significant effects on planktotrophic echinoderm larvae. The qualitative effect of starvation on the condition of echinoderm larvae prior to and during settlement was confirmed by Basch & Pearse (1995), who demonstrated a strong effect on larval size, development, swimming and substrate searching behaviour of the asteroid *Asterina miniata*. Likewise, Pratchett et al. (2017) reported delays in peak settlement of *Acanthaster cf. solaris* at low food levels, which are likely reflective of delays in larval development. Thus, even if direct mortality due to starvation is unlikely under natural conditions, prolonged planktonic existence may increase the risk of predation and thus lead to higher total mortality, or advection to less suitable settlement sites (Thorson 1950). Conversely, a shortened planktonic phase, due to early metamorphosis of less developed echinoderm larvae in response to settlement cues, may also increase total mortality within a cohort of echinoderms (Mos & Dworjanyn 2016).

While a range of abiotic and biotic factors can influence the abundance and distribution of larval echinoderms, and thus the temporal and spatial variation in the supply of competent larvae, the individual roles and combined effect of these processes on larval settlement remain unclear. Further adding complexity to this puzzle, larval cloning has been described for some echinoderms (Balsler 1998, Allen et al. 2019, Hart et al. 2021). If supported by environmental conditions, cloning has the potential to influence dispersal distance of planktonic larval stages and increase the number of larvae reaching metamorphic competence (Allen et al. 2019), which, in turn, may influence rates of settlement and recruitment (Hart et al. 2021).

Species with complex, planktonic, feeding larvae are common across all echinoderm classes, with the exception of crinoids (McEdward & Miner 2001, Uthicke et al. 2009). However, all five classes also possess lecithotrophic larval types in both planktonic and benthic developmental habitats (McEdward & Miner 2001, Raff & Byrne 2006, Byrne & O'Hara 2017), with benthic development and brooding documented in some echinoids (Emllet et al. 1987), crinoids (Lahaye & Jangoux 1985), holothuroids (McEuen 1986) and ophiuroids (Ebert 1983). Importantly, the dispersal, condition and survival of planktonic echinoderm larvae appears to be governed by a suite of abiotic and biotic variables, which will, in turn, affect spatiotemporal patterns of settlement (Basch & Pearse 1995). When analysing the drivers of settlement patterns, however, the capability for long-distance dispersal also needs to be considered, especially for species with prolonged planktonic phases, as

observed in asteroids of the genus *Luidia* which are known to spend >1 year in the water column as exceptionally large post-larvae (Wilson 1978, Domanski 1984).

Metamorphic competence and substratum search

Metamorphic competence is the developmental capacity of larvae to undergo complete morphogenesis that is necessary for settlement including metamorphosis (Hadfield et al. 2001). Such competence is conditional upon complete larval development, which requires a minimum prescribed, but species-specific, pre-competency period (Sutherby et al. 2012). Larval developmental rates and the minimum pre-competency period are, however, influenced by nutritional resources and temperature (Lucas 1982, Hadfield et al. 2001). In general, most planktotrophic larvae in the pelagic habitat attain competence after a few weeks to several months. For example, planktotrophic larvae of the echinoid *Strongylocentrotus purpuratus* acquire metamorphic competence after 4–6 weeks post-fertilisation (Strathmann 1987). Lecithotrophic echinoderm larvae may acquire competence within days (Pawlik 1992, Hadfield et al. 2001). Another echinoid, *Heliocidaris erythrogramma*, for example, has a highly reduced larva, which develops from large eggs and attains metamorphic competence within 3–6 days (Byrne et al. 2001).

While metamorphic (or settlement) competence is conditional upon larval development, metamorphosis itself is often induced by specific environmental conditions or cues (as discussed later). Importantly, echinoderm larvae may attain competence long before they actually settle, deferring metamorphosis until settlement opportunities present (Birkeland et al. 1971, Hadfield et al. 2001, Pratchett et al. 2017). Extended competency periods are particularly pronounced for planktotrophic larvae (Hadfield et al. 2001), with larvae remaining in the water column until the presence of suitable habitat is signalled by abiotic or biotic cues, as opposed to immediate metamorphosis in a potentially unsuitable habitat. For example, short-term exposure to turbulence signalling proximity to reefs can cause echinoid larvae to immediately transition from a pre-competent to a competent state (Gaylord et al. 2013, Hodin et al. 2015, Ferner et al. 2019), which allows them to respond to chemical cues before and after they contact the substratum (Hodin et al. 2020). Similarly, histamine, a compound associated with various marine algae, has been shown to modulate metamorphic competence in *Strongylocentrotus purpuratus* (Sutherby et al. 2012). At the same time, this organic compound is hypothesised to maintain the developmental priming of competence once larvae are morphologically competent by inhibiting settlement in the absence of suitable cues (Sutherby et al. 2012). More specifically, histamine achieves the maintenance of competency in echinoid larvae by inhibiting caspase-mediated apoptosis (Sutherby et al. 2012), and thus suppressing the destruction of larval-specific structures necessary to settle and metamorphose until a suitable settlement site is found.

Throughout this competency period, larvae continue to live a functional planktonic life until it culminates in either passive deposition onto the substratum, or active selection of a suitable habitat/substratum (Figure 1). Likewise, larvae are thought to delay settlement in response to cues indicative of an unsuitable settlement site (Hadfield & Paul 2001), although inhibitory cues have rarely been explored in echinoderm studies. All ophiuroids and some groups of asteroids and holothuroids metamorphose in the plankton and then often settle indiscriminately (Wilson 1978, Domanski 1984, Hendler 1991, Komatsu et al. 2000, McEdward & Miner 2001, Selvakumaraswamy & Byrne 2004, Morgan & Jangoux 2005). However, other echinoderm larvae with a planktonic larval phase generally require physical or chemical settlement cues and subsequent contact with the substratum in order to metamorphose (Hadfield & Paul 2001). Once a larva has the ability to discriminate cues, substratum choice appears to be primarily limited by the availability of suitable substrata, and the availability and concentration of pertinent cues in the water column. Waterborne chemical cues originating from conspecifics (Pearce & Scheibling 1990a, Dworjanyan & Pirozzi 2008) and various

algal substrata (Williamson et al. 2000, Swanson et al. 2004) have been demonstrated to initiate settlement and subsequent metamorphosis in echinoderm taxa. Such cues can be highly specific (Table 1) and are mostly detected in relatively close proximity to their source organisms.

Passive transport is generally thought to be the major determinant in the dispersal of echinoderm larvae over broad spatial scales. Echinoid larvae are hypothesised to also use environmental signposts such as turbulence to narrow down potential areas of settlement at relatively localised scales (Gaylord et al. 2013, Hodin et al. 2020). Short-term behavioural responses of echinoid larvae to such signposts include the cessation of swimming, which facilitates sinking and contact with the substratum (Ferner et al. 2019). Although direct evidence of active vertical movement is sparse, the extremely fast sinking and substratum attachment in response to inductive settlement cues (Tables 1 and 2) suggests that most competent echinoderm larvae do not randomly or passively sink to the bottom. Rapid sinking may also be a response to the high densities of planktivorous invertebrates and fish that associate with the substratum (Tegner & Dayton 1981, Balch & Scheibling 2001).

Other key physical variables with the potential to substantially alter settlement patterns are temperature and pH (Mos et al. 2011, Li et al. 2011b). Settlement pulses in echinoids, holothuroids and ophiuroids have been linked to temperature peaks and fluctuations (Balch et al. 1999, García-Sanz et al. 2014, Sotelo-Casas et al. 2016, Glockner-Fagetti & Phillips 2020). For example, larval settlement of the echinoid *Strongylocentrotus purpuratus* in southern California was orders of magnitude lower during warm, El Niño conditions (Okamoto et al. 2020), while settlement of *Diadema africanum* was found to be high during warm years in the Canary Islands (Hernández et al. 2010). However, these links could be driven by other factors, such as spawning induced by temperature change (Caballes & Pratchett 2017, Caballes et al. 2021), and need to be explicitly tested in field and laboratory experiments. In a laboratory study, settlement of the echinoid *Tripneustes gratilla* was unaffected by temperatures between 24 and 30°C, but was substantially reduced at 33°C (Mos et al. 2011). Likewise, warmer temperatures reduced settlement rates in the holothuroid *Apostichopus japonicus* (Li et al. 2011b) and negatively affected development in settlement-stage individuals of the echinoid *Heliocidaris erythrogramma* (Byrne et al. 2011). Moreover, reduced settlement rates at lowered pH have been demonstrated in some echinoids (García et al. 2015), asteroids (e.g. Uthicke et al. 2013) and holothuroids (e.g. Li et al. 2011b). Low pH negatively affected morphological traits, but not settlement rates in the echinoid *Centrostephanus rodgersii*; however, high pH reduced settlement rates considerably (Mos et al. 2020). Conversely, the echinoids *Evechinus chloroticus* (Espinell-Velasco et al. 2020) and *Pseudechinus huttoni* (Houlihan et al. 2020) appeared unaffected by changes in pH. Settlement was delayed at reduced pH in the echinoid *Paracentrotus lividus* (García et al. 2015), but not in *Arbacia lixula* (Wangensteen et al. 2013) and *Heliocidaris erythrogramma* (Byrne et al. 2011). Espinell-Velasco et al. (2018) and Nelson et al. (2020) argued that decreases in seawater pH may affect microbial communities and thus also indirectly alter the settlement of echinoderms that respond to cues associated with biofilms. On balance, both passive processes and active vertical migration in response to environmental cues appear to play significant, but highly variable roles between the attainment of competence and the first contact with the substratum in planktonic echinoderm larvae.

Substratum contact, exploration and selection

Once a competent larva has found its way to the substratum, contact is established and attachment of the larva to the surface of the substratum occurs (Yamaguchi 1973, Hamel & Mercier 1996, Gosselin & Jangoux 1998). For many sessile marine invertebrates, attachment to a substratum may already represent the initiation of metamorphosis into their juvenile form (Hadfield & Paul 2001). Conversely, many motile species, including echinoderms, have the ability to detach and reattach to substrata while delaying metamorphosis and exploring the suitability of various settlement

LARVAL SETTLEMENT IN ECHINODERMS

Table 1 Summary of natural chemical cues known to induce larval settlement and metamorphosis in echinoderm classes and species

Chemical stimulus	Class	Species	Reference
Gregarious settlement cues			
Peptide	Echinoidea	<i>Dendraster excentricus</i>	Highsmith (1982), Burke (1984), Highsmith & Emlet (1986)
Not characterised	Echinoidea	<i>Echinarachnius parma</i> , <i>Scaphechinus mirabilis</i> , <i>Tripneustes gratilla</i>	Highsmith & Emlet (1986), Pearce & Scheibling (1990a), Takeda (2008), Dworjanyan & Pirozzi (2008), Mos et al. (2011)
	Ophiuroidea	<i>Ophiothrix fragilis</i>	Warner (1971), Morgan & Jangoux (2004), Morgan & Jangoux (2005)
	Holothuroidea	<i>Molpadia intermedia</i> , <i>Psolus chitonoides</i>	Young & Chia (1982), McEuen & Chia (1985)
	Crinoidea	<i>Antedon bifida</i> , <i>Florometra serratissima</i> , <i>Dorometra sesokonis</i>	Mladenov & Chia (1983), Lahaye & Jangoux (1985), Obuchi et al. (2010)
Associative settlement cues			
Seagrass			
<i>Enhalus acoroides</i>	Holothuroidea	<i>Holothuria scabra</i>	Mercier et al. (2000), Agudo (2007)
<i>Halophila ovalis</i>	Echinoidea	<i>Holopneustes purpurascens</i> , <i>H. inflatus</i>	Swanson et al. (2012)
<i>Posidonia australis</i>	Echinoidea	<i>Holopneustes purpurascens</i> , <i>H. inflatus</i>	Swanson et al. (2012)
<i>Posidonia oceanica</i>	Echinoidea	<i>Paracentrotus lividus</i>	Privitera et al. (2011)
<i>Thalassia hemprichii</i>	Holothuroidea	<i>Holothuria scabra</i>	Mercier et al. (2000), Agudo (2007)
<i>Zostera capricorni</i>	Echinoidea	<i>Holopneustes purpurascens</i> , <i>H. inflatus</i>	Swanson et al. (2012)
Red algae			
<i>Chondrus crispus</i>	Echinoidea	<i>Strongylocentrotus droebachiensis</i>	Pearce & Scheibling (1991)
<i>Delisea pulchra</i>	Echinoidea	<i>Holopneustes purpurascens</i>	Williamson et al. (2000), Swanson et al. (2004, 2006)
Carbohydrate		<i>Holopneustes purpurascens</i>	Williamson et al. (2000)
<i>Floridoside-isethionic acid</i>			
Histamine		<i>Holopneustes purpurascens</i> , <i>H. inflatus</i> , <i>Heliocidaris erythrogramma</i> , <i>Centrostephanus rogersii</i>	Swanson et al. (2004, 2006, 2012)
<i>Laurencia rigida</i>	Echinoidea	<i>Holopneustes purpurascens</i>	Williamson et al. (2000)
<i>Laurencia obtusa</i> , <i>L. rigada</i> , <i>Laurencia</i> sp.	Echinoidea	<i>Centrostephanus rogersii</i> , <i>Tripneustes gratilla</i>	Dworjanyan & Pirozzi (2008), Swanson et al. (2012)
<i>Mastocarpus stellatus</i>	Echinoidea	<i>Strongylocentrotus droebachiensis</i>	Pearce & Scheibling (1991)
<i>Palmaria palmata</i>	Echinoidea	<i>Strongylocentrotus droebachiensis</i>	Pearce & Scheibling (1991)
<i>Polysiphonia harveyi</i> , <i>P. lanosa</i>	Echinoidea	<i>Strongylocentrotus droebachiensis</i>	Pearce & Scheibling (1991)
<i>Solieria robusta</i>	Echinoidea	<i>Holopneustes purpurascens</i>	Williamson et al. (2000)

(Continued)

Table 1 (Continued) Summary of natural chemical cues known to induce larval settlement and metamorphosis in echinoderm classes and species

Chemical stimulus	Class	Species	Reference
Red algal turf	Echinoidea	<i>Strongylocentrotus purpuratus</i> , <i>Paracentrotus lividus</i>	Rowley (1989), Privitera et al. (2011)
Coralline red algae			
<i>Amphiroa anceps</i>	Echinoidea	<i>Centrostephanus rodgersii</i> , <i>Holopneustes purpurascens</i> , <i>H. inflatus</i> , <i>Heliocidaris</i> <i>erythrogramma</i> , <i>Tripneustes</i> <i>gratilla</i>	Williamson et al. (2000), Huggett et al. (2006) Swanson et al. (2006, 2012), Dworjanyan & Pirozzi (2008)
<i>Corallina elongata</i>	Echinoidea	<i>Arbacia lixula</i> , <i>Echinocardium</i> <i>cordatum</i> , <i>Paracentrotus lividus</i>	Nunes & Jangoux (2008), Privitera et al. (2011)
<i>Corallina pilulifera</i>	Echinoidea	<i>Pseudocentrotus depressus</i> , <i>Anthocidaris crassisipina</i>	Kitamura et al. (1992, 1993, 1994)
Polyunsaturated fatty acids			Kitamura et al. (1993, 1994)
Eicosapentaenoic acid			Kitamura et al. (1993)
Arachidonic acid			Kitamura et al. (1993)
Dihomo- γ -linolenic acid			Kitamura et al. (1994)
Eicosatrienoic acid			Kitamura et al. (1994)
<i>Corallina officinalis</i>	Echinoidea	<i>Centrostephanus rodgersii</i> , <i>Heliocidaris erythrogramma</i> , <i>Holopneustes purpurascens</i> , <i>Strongylocentrotus</i> <i>droebachiensis</i> , <i>Tripneustes</i> <i>gratilla</i>	Pearce & Scheibling (1990b, 1991), Williamson et al. (2000), Huggett et al. (2006), Dworjanyan & Pirozzi (2008), Mos et al. (2011), Swanson et al. (2012)
<i>Corallina</i> sp.	Echinoidea	<i>Evechinus chloroticus</i>	Lamare & Barker (2001)
<i>Lithothamnion californicum</i>	Echinoidea	<i>Strongylocentrotus purpuratus</i>	Rowley (1989)
<i>Lithothamnion glaciale</i>	Echinoidea	<i>Strongylocentrotus droebachiensis</i>	Pearce & Scheibling (1990b, 1991)
<i>Lithothamnium</i> sp. (likely <i>Lithothamnion proliferum</i>)	Asteroidea	<i>Acanthaster</i> cf. <i>solaris</i>	Johnson et al. (1991), Johnson & Sutton (1994), Uthicke et al. (2018)
<i>Lithophyllum incrustans</i>	Echinoidea	<i>Arbacia lixula</i> , <i>Paracentrotus</i> <i>lividus</i>	Privitera et al. (2011)
<i>Lithophyllum yessoense</i>	Echinoidea	<i>Strongylocentrotus nudus</i>	Taniguchi et al. (1994)
Dibromomethane			Taniguchi et al. (1994)
<i>Mesophyllum insigne</i>	Asteroidea	<i>Stichaster australis</i>	Barker (1977)
<i>Neogoniolithon fosliei</i>	Asteroidea	<i>Acanthaster</i> cf. <i>solaris</i>	Johnson et al. (1991)
<i>Phymatolithon laevigatum</i> , <i>R. rugulosum</i>	Echinoidea	<i>Strongylocentrotus droebachiensis</i>	Pearce & Scheibling (1990b)
Coralline red algae spp.	Echinoidea	<i>Echinometra mathaei</i> , <i>E. oblonga</i> , <i>E. spp.</i> , <i>Strongylocentrotus</i> <i>droebachiensis</i> , <i>Tripneustes</i> <i>gratilla</i>	Rahman & Uehara (2001), Dworjanyan & Pirozzi (2008), Scheibling & Robinson (2008)
Non-coralline crustose red algae			
<i>Hildenbrandia rubra</i>	Echinoidea	<i>Strongylocentrotus droebachiensis</i>	Pearce & Scheibling (1991)

(Continued)

LARVAL SETTLEMENT IN ECHINODERMS

Table 1 (Continued) Summary of natural chemical cues known to induce larval settlement and metamorphosis in echinoderm classes and species

Chemical stimulus	Class	Species	Reference
Brown algae			
<i>Dictyota dichotoma</i>	Echinoidea	<i>Centrostephanus rodgersii</i> , <i>Tripneustes gratilla</i>	Dworjanyn & Pirozzi (2008) Swanson et al. (2012)
<i>Dilophus marginatus</i>	Echinoidea	<i>Centrostephanus rodgersii</i> , <i>Tripneustes gratilla</i>	Dworjanyn & Pirozzi (2008), Swanson et al. (2012)
<i>Ecklonia radiata</i>	Echinoidea	<i>Heliocidaris erythrogramma</i> , <i>Holopneustes purpurascens</i> , <i>Tripneustes gratilla</i>	Huggett et al. (2006), Swanson et al. (2006), Dworjanyn & Pirozzi (2008)
<i>Fucus distichus</i>	Echinoidea	<i>Strongylocentrotus droebachiensis</i>	Pearce & Scheibling (1991)
<i>Homeostrictichus olsenii</i>	Echinoidea	<i>Holopneustes purpurascens</i> , <i>Tripneustes gratilla</i>	Swanson et al. (2006), Dworjanyn & Pirozzi (2008)
<i>Laminaria digitata</i> & <i>L. longicuris</i>	Echinoidea	<i>Strongylocentrotus droebachiensis</i>	Pearce & Scheibling (1991)
<i>Pylaiella littoralis</i>	Echinoidea	<i>Strongylocentrotus droebachiensis</i>	Pearce & Scheibling (1991)
<i>Sargassum linearifolium</i>	Echinoidea	<i>Centrostephanus rodgersii</i> , <i>Heliocidaris erythrogramma</i> , <i>Tripneustes gratilla</i>	Huggett et al. (2006), Dworjanyn & Pirozzi (2008), Mos et al. (2011), Swanson et al. (2012)
<i>Sargassum vestitum</i>	Echinoidea	<i>Heliocidaris erythrogramma</i>	Huggett et al. (2006)
<i>Sargassum</i> sp.	Echinoidea	<i>Tripneustes gratilla</i>	Juinio-Meñez & Bangi (2010)
	Holothuroidea	<i>Holothuria scabra</i>	Agudo (2007)
<i>Stypocaulon scoparium</i>	Echinoidea	<i>Paracentrotus lividus</i>	Privitera et al. (2011)
<i>Zonaria angustata</i>	Echinoidea	<i>Tripneustes gratilla</i>	Dworjanyn & Pirozzi (2008)
Green algae			
<i>Codium fragile</i>	Echinoidea	<i>Heliocidaris erythrogramma</i>	Huggett et al. (2006)
<i>Enteromorpha linza</i>	Echinoidea	<i>Paracentrotus lividus</i>	Gosselin & Jangoux (1996)
<i>Enteromorpha</i> sp.	Echinoidea	<i>Strongylocentrotus droebachiensis</i>	Pearce & Scheibling (1991)
<i>Spongomorpha aeruginosa</i>	Echinoidea	<i>Strongylocentrotus droebachiensis</i>	Pearce & Scheibling (1991)
<i>Ulva lactuca</i>	Echinoidea	<i>Tripneustes gratilla</i>	Dworjanyn & Pirozzi (2008)
Endophytic microalgae			
<i>Ulva lens</i>	Echinoidea	<i>Apostichopus japonicas</i> , <i>Strongylocentrotus nudus</i>	Taniguchi et al. (1994), Takahashi et al. (2002), Matsuura et al. (2009)
Dibromomethane	Echinoidea	<i>Strongylocentrotus nudus</i>	Taniguchi et al. (1994)
Glycoglycerolipids	Echinoidea	<i>Strongylocentrotus intermedius</i> , <i>S. nudus</i>	Takahashi et al. (2002)
Polychaete			
<i>Phyllochaetopterus prolifica</i>	Asteroidea	<i>Mediaster aequalis</i>	Birkeland et al. (1971), Bryan (2004)
Biofilm-associated cues			
Bacteria			
<i>Photobacterium phosphoreum</i>	Echinoidea	<i>Holopneustes purpurascens</i>	Swanson et al. (2006)
<i>Photobacterium</i> spp.	Echinoidea	<i>Heliocidaris erythrogramma</i>	Huggett et al. (2006)
<i>Pseudoalteromonas</i> <i>luteoviolacea</i> , other <i>Pseudoalteromonas</i> spp.	Echinoidea	<i>Heliocidaris erythrogramma</i>	Huggett et al. (2006)
<i>Shewanella</i> spp.	Echinoidea	<i>Heliocidaris erythrogramma</i>	Huggett et al. (2006)

(Continued)

Table 1 (Continued) Summary of natural chemical cues known to induce larval settlement and metamorphosis in echinoderm classes and species

Chemical stimulus	Class	Species	Reference
<i>Thalassomonas viridans</i>	Echinoidea	<i>Holopneustes purpurascens</i>	Swanson et al. (2006)
<i>Vibrio</i> spp.	Echinoidea	<i>Heliocidaris erythrogramma</i>	Huggett et al. (2006)
Other/unspecified bacteria	Echinoidea	<i>Arachnoides placenta</i> , <i>Arbacia punctulata</i> , <i>Heliocidaris erythrogramma</i> , <i>Lytechinus pictus</i> , <i>Tripneustes gratilla</i>	Cameron & Hinegardner (1974), Huggett et al. (2006), Dworjanyn & Pirozzi (2008), Mos et al. (2011)
	Asteroidea	<i>Acanthaster cf. solaris</i>	Johnson et al. (1991), Johnson & Sutton (1994)
Periphytic diatoms			
<i>Achnanthes</i> sp.	Holothuroidea	<i>Apostichopus japonicus</i>	Ito & Kitamura (1997)
<i>Amphora</i> sp.	Holothuroidea	<i>Apostichopus japonicus</i>	Ito & Kitamura (1997)
<i>Navicula</i> sp.	Holothuroidea	<i>Holothuria scabra</i> , <i>Apostichopus japonicus</i>	Ito & Kitamura (1997), Agudo (2007)
<i>Nitzschia</i> spp.	Echinoidea	<i>Tripneustes gratilla</i>	Mos et al. (2011)
	Holothuroidea	<i>Holothuria scabra</i> , <i>Apostichopus japonicus</i>	Ito & Kitamura (1997), Agudo (2007)
<i>Platymonas</i> sp.	Holothuroidea	<i>Holothuria scabra</i>	Agudo (2007)
Multiple species (predominantly <i>Navicula</i> , <i>Amphora</i> , <i>Achnanthes</i> & <i>Nitzschia</i> spp.)	Echinoidea	<i>Anthocidaris crassispina</i> , <i>Pseudocentrotus depressus</i>	Rahim & Kitamura (2004)
Unspecified biofilm	Echinoidea	<i>Anthocidaris crassispina</i> , <i>Evechinus chloroticus</i> , <i>Pseudocentrotus depressus</i> , <i>Tripneustes gratilla</i>	Lamare & Barker (2001), Rahim & Kitamura (2004), Mos et al. (2011)
	Asteroidea	<i>Stichaster australis</i> , <i>Coscinasterias calamaria</i>	Barker (1977)

sites (Crisp 1984, Hadfield & Paul 2001, Scheibling & Robinson 2008, Vellutini & Migotto 2010). Competent larvae of the crown-of-thorns starfish *Acanthaster cf. solaris* (Figure 2) have been observed to drift downwards and flex the anterior body dorsally to orient their brachiolar arms towards the substratum in an attempt to test the suitability of substratum surfaces for settlement (Yamaguchi 1973). Similarly, the asteroid *Patiriella regularis* swims along the substratum surface and exhibits searching behaviour using its median brachium (Byrne & Barker 1991). Echinoid larvae (*Paracentrotus lividus*) interrupt the beatings of their epaulette cilia to reach the substratum, which is then tested by primary podia (Gosselin & Jangoux 1998, Flammang et al. 1998). Without appropriate cues, the larvae fold back their podia and ascend back into the water column via ciliary beating of the epaulettes (Gosselin & Jangoux 1998). In crinoids, the adhesive pit serves to attach the larval body to the substratum by developing the attachment disc of a juvenile (McEdward & Miner 2001). Upon first substratum contact with its tentacles, the holothuroid *Cucumaria frondosa* spent up to 40 hours searching the substratum surface for a suitable settlement site using its ambulacral podia (Hamel & Mercier 1996).

In most cases, specificity in echinoderm settlement is mediated by chemical cues associated with the biogenic substrate (Pawlik 1992, Hadfield & Paul 2001, Dworjanyn & Pirozzi 2008). Evidence of the inductive capacity of cues associated with conspecifics (e.g. Pearce & Scheibling 1990a), prey (e.g. Birkeland et al. 1971), algae (e.g. Williamson et al. 2020) and biofilms (Huggett et al. 2006) is highly abundant for echinoderms (Table 1). When such cues signal the suitability of

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Table 2 Summary of ‘artificial’ chemical cues (i.e. neurotransmitters and ions) known to induce larval settlement and metamorphosis in echinoderm classes and species

Compound	Class	Species	Reference
Amino acid derivatives			
Glutamine	Echinoidea	<i>Scaphechinus mirabilis</i> , <i>Strongylocentrotus intermedius</i> , <i>Pseudocentrotus depressus</i>	Yazaki & Harashima (1994), Naidenko (1996)
γ-Amino butyric acid (GABA)	Echinoidea	<i>Echinometra mathaei</i> , <i>E. oblonga</i> , <i>E.</i> spp., <i>Strongylocentrotus</i> <i>droebachiensis</i>	Pearce & Scheibling (1990a), Rahman & Uehara (2001)
	Asteroidea	<i>Mediaster aequalis</i>	Bryan (2004)
	Holothuroidea	<i>Apostichopus japonicus</i> <i>Holothuria scabra</i>	Sun et al. (2014) Nontunha et al. (2021)
Glutamic acid	Echinoidea	<i>Scaphechinus mirabilis</i> , <i>Strongylocentrotus intermedius</i>	Naidenko (1996)
Monosodium glutamate	Holothuroidea	<i>Holothuria scabra</i>	Nontunha et al. (2021)
Tyrosine derivatives			
Dopamine	Echinoidea	<i>Dendraster excentricus</i>	Burke (1983b)
	Holothuroidea	<i>Apostichopus japonicus</i> , <i>Holothuria</i> <i>scabra</i>	Matsuura et al. (2009), Sun et al. (2014), Nontunha et al. (2021)
L-3,4- Dihydroxyphenylalanine (L-DOPA)	Echinoidea	<i>Dendraster excentricus</i>	Burke (1983b)
	Holothuroidea	<i>Apostichopus japonicus</i> <i>Holothuria scabra</i>	Matsuura et al. (2009), Sun et al. (2014) Nontunha et al. (2021)
Epinephrine	Holothuroidea	<i>Apostichopus japonicus</i>	Matsuura et al. (2009)
Norepinephrine	Holothuroidea	<i>Apostichopus japonicus</i>	Matsuura et al. (2009) Sun et al. (2014)
Choline derivative			
Acetylcholine	Holothuroidea	<i>Apostichopus japonicus</i>	Sun et al. (2014)
Ions			
K ⁺	Echinoidea	<i>Clypeaster rosaceus</i> , <i>Colobocentrotus atratus</i> , <i>Dendraster excentricus</i> , <i>Diadema</i> <i>antillarum</i> , <i>Echinarachnius parma</i> , <i>Echinometra lucunter</i> , <i>E. viridis</i> , <i>Heterocentrotus mamallatus</i> , <i>Leodia sexiesperforata</i> , <i>Lytechinus</i> <i>variegatus</i> , <i>Mellita tenuis</i> , <i>Mesocentrotus franciscanus</i> , <i>Strongylocentrotus droebachiensis</i> , <i>S. fragilis</i> , <i>S. pallidus</i> , <i>S. purpuratus</i>	Cameron et al. (1989), Pearce & Scheibling (1994), Carpizo-Ituarte et al. (2002), Heyland et al. (2004, 2006), Heyland & Hodin (2004), Gaylord et al. (2013), Hodin et al. (2015, 2019)
	Holothuroidea	<i>Apostichopus japonicus</i>	Sun et al. (2014)
Ca ²⁺	Echinoidea	<i>Lytechinus variegatus</i>	Cameron et al. (1989)
NH ₄ ⁺	Holothuroidea	<i>Apostichopus japonicus</i>	Sun et al. (2014)

a site, the cascade of settlement events, comprising initial adhesion (Crisp 1984) and metamorphic morphogenesis of echinoderm larvae, can occur rapidly (Juinio-Meñez & Bangi 2010, Swanson et al. 2012). If, however, no inductive cue is present, the explorative period may be prolonged (Hamel & Mercier 1996), and competent larvae may swim off in a broad-scale search for other surfaces. As a result, a larva may risk being exposed to benthic and sometimes planktonic predators during this period (Tegner & Dayton 1981, Cowan et al. 2016a,b), but the trade-off is an increased chance of settlement and post-metamorphic success.

Although their importance appears to be secondary to chemical cues, physical factors, such as light intensity and the physical properties associated with the substratum, may also play a significant role in settlement induction once a competent larva has contacted the substratum surface (Young & Chia 1984, Privitera et al. 2011). More specifically, sedimentation, the contour, microtopography, texture, exposure and the thermal capacity of a substratum may affect where competent larvae choose to settle, depending on taxon-specific habitat requirements and cue responsiveness (Young & Chia 1984, Walters & Wetthey 1991, Hamel & Mercier 1996). For example, fine sediments have been identified as a potential inhibitor of settlement for *Evechinus chloroticus* (Phillips & Shima 2006, Walker 2007), while larvae of the crown-of-thorns starfish *Acanthaster cf. solaris* are thought to favour particular substrata because their rough texture and depressions suit their metamorphosing larvae (Lucas 1974, Ormond & Campbell 1974). Other asteroids (Barker 1977, Barker & Nichols 1983, Metaxas et al. 2008) and holothuroids (Hamel & Mercier 1996) predominantly settle on the underside of rocks and rubble. This pattern of substratum selectivity may be linked to light exposure, as settlers of the holothuroid *Cucumaria frondosa* not only showed strong selectivity for the undersides of the physical substratum, but were highly sensitive to light (Hamel & Mercier 1996). When exposed to light, settlement of *C. frondosa* larvae was highest on rocky substrates with crevices, relatively high on gravel and smooth rocky substrates and substantially lower on mud, sand and glass (Hamel & Mercier 1996). Largely photopositive during their exploration and substratum selection, these larvae were observed to rapidly change their initial site of substratum contact and move to light sheltered areas on the substratum (Hamel & Mercier 1996). Similarly, *Patiriella regularis* asteroids settle on the undersides of substrata and appear to be light sensitive during the settlement phase (Byrne & Barker 1991). Given the generally high prevalence of light sensitivity across this phylum (Byrne & O'Hara 2017), light availability and intensity are likely also to play an underappreciated role in the substratum search and selection by other echinoderm groups.

Larval metamorphosis

Upon reception of metamorphic cues, larval metamorphosis, a complex network of cellular processes which involve the transformation and reorganisation of most tissues and cells, is induced (Figure 3, Pearse & Cameron 1991, Morgan & Jangoux 2005). All ophiuroids, and some asteroids, holothurians and echinoids are able to metamorphose in the water column and sink to the substratum in their juvenile form (Wilson 1978, Domanski 1984, Hendler 1991, McEdward & Miner 2001, Morgan & Jangoux 2005, Selvakumaraswamy & Byrne 2006). However, crinoids and most asteroid, echinoid and holothuroid groups, including the ecologically and economically important taxa discussed in this review, generally attach to a substratum prior to metamorphosis (Pearse & Cameron 1991, McEdward & Miner 2001). Metamorphosis in echinoderms begins with a larva initiating the degeneration of larva-specific characters and ends once all juvenile characters have emerged and the juvenile is fully functioning in its (usually benthic) habitat (*sensu* Hadfield et al. 2001). In general, this includes a transformation of the fundamental bilateral symmetry of echinoderm larvae into a juvenile form with a radial symmetry (Figures 2 and 3, McEdward & Miner 2001). The numerous morphogenic events occurring during this period have been documented for some species, including echinoids (e.g. Mazur & Miller 1971), asteroids (e.g. Caballes & Pratchett 2014) and ophiuroids (e.g. Morgan & Jangoux 2005), and have been reviewed in detail for Echinoidea (e.g. Burke

1983a, Pearse & Cameron 1991). For example, competent (late brachiolaria) larvae of the asteroid *Acanthaster cf. solaris* attach to the substratum surface and metamorphose into their juvenile form by absorbing the larval body into the asteroid (Figure 2). Similarly, most echinoids must undergo substantial physiological changes concomitant with the transition from a pelagic and planktotrophic larva to a benthic and herbivorous juvenile (Figure 3).

Neural mechanisms for the induction of echinoderm metamorphosis have been supported by multiple lines of evidence (Sutherby et al. 2012, Caballes and Pratchett 2014). Specifically, neurons in the apical organ of competent echinoid larvae are suggested to detect exogenous metamorphic cues and translate that information into behavioural and physiological responses (Burke 1979, 1983b, Brandhorst et al. 2001). However, little is known about the causal relationships among the various cellular processes occurring during metamorphic transformation. In echinoids, inductive cues are likely transduced by epithelial cells via Ca^{2+} -dependent K^+ conductance, triggering the involution of the larval epithelium (Emler 1988, Pearse & Cameron 1991). Few superficial organs have been characterised in echinoid larvae; however, cues for the nerve cells may be received through sensory cells on the surface of the podia of the echinoid rudiment (Burke 1980, Smith et al. 2008, Ullrich-Lüter et al. 2011, Valero-Garcia et al. 2016, Marconi et al. 2019). At the same time, the eversion of the urchin rudiment causes the musculoepithelial cells to contract, which alters its shape and everts the rudiment (Pearse & Cameron 1991, Vellutini & Migotto 2010). Once the larval epithelium is fully collapsed, the adult epithelium fuses on the aboral surface (Pearse & Cameron 1991, Vellutini & Migotto 2010). The enclosed larval cells then lose their attachments and degenerate (Cameron 1975, Chia & Burke 1978). Some tissues documented to break down soon after the start of metamorphosis include the epidermis, oesophagus, epaulettes, larval mouth and the ciliary bands, while the skeletal mesenchyme and larval gut are transformed into adult tissues (Chia & Burke 1978, Burke 1983a). Similar transformations occur in other echinoderm larvae, including many asteroids, echinoids and ophiuroids, which see adult rudiments unfolded and the larval body involuted into what will become the aboral surface of the juvenile body (Figure 3, Burke 1993a, Hadfield et al. 2001). In crinoids, the vestibule and associated ventral structures rotate towards the posterior end of the larvae; however, metamorphic transformations do not include a distinct adult rudiment oriented orthogonally to the larval plane of symmetry (Figure 3, McEdward & Miner 2001). Altogether, the complex network of these metamorphic processes, which are variable among taxa, transforms competent echinoderm larvae into fully functioning juveniles, which, in most cases, are able to live, move and feed in their benthic habitat.

Post-settlement processes

Newly settled echinoderms are generally subject to very high mortality within the first weeks to months of their benthic life stage (Gosselin & Qian 1997, Hunt & Scheibling 1997, Balch & Scheibling 2001). As such, our understanding of post-settlement processes is critical to determine how patterns established at settlement are altered, and the consequent effects on adult populations (Underwood & Fairweather 1989). Recruitment to juvenile and adult populations is highly variable in echinoderms, both temporally and spatially (reviewed by Ebert 1983, Balch & Scheibling 2001, Ebert 2021b), and plays a vital role in the dynamics of echinoderm populations and, in the case of ecologically important taxa, may substantially alter marine ecosystems (McClanahan 1988, Bonaviri et al. 2012, Pratchett et al. 2014). Settlement rates do not always explain patterns of distribution and abundance of conspecific juveniles and adults (Loosanoff 1964, Rowley 1989, Vermeij et al. 2010, Williams et al. 2010, 2011, Rogers & Lorenzen 2016), and adult population dynamics may be driven by early post-settlement processes, including high mortality rates soon after settlement. In the case of *Diadema antillarum* in the southern Caribbean Sea, for example, unknown sources of high post-settlement mortality may have prevented a recovery of the local adult population following the 1983 die-off, despite a substantial recovery of settlement rates (Vermeij et al. 2010).

The vast majority of early post-settlement mortality in echinoderms has been attributed to various invertebrate and fish predators (Sala & Zabala 1996, Sala et al. 1998, Hereu et al. 2005, Pederson & Johnson 2006, Clemente et al. 2009, Bonaviri et al. 2012, Cowan et al. 2017, Keesing et al. 2018). Small, recently emerged size classes are often most vulnerable to predation (McClanahan & Muthiga 1989, Pederson & Johnson 2006, Clemente et al. 2007, Ling & Johnson 2009), such as the size-dependent predation by rock lobsters on the kelp overgrazing echinoids *Heliocidaris erythrogramma* and *Centrostephanus rodgersii* (Pederson & Johnson 2006, Ling et al. 2009). Other factors that may contribute to the loss of post-settlement echinoderms from populations include starvation (Keesing and Halford 1992), disease (Hughes et al. 1985, Lessios 1988), abiotic disturbances (Cameron & Fankboner 1989), space competition (Hamel & Mercier 1996) and migration (Young & Chia 1982, Hamel & Mercier 1996), although movement over large distances is rare for small post-settlement juveniles (Rowley 1989). Of all post-settlement processes, mortality is generally viewed as having the greatest effect on recruitment to juvenile populations, but determining the relative contributions of these processes in the field has proven to be challenging (Andrew & Choat 1985, Balch & Scheibling 2001). Few studies have assessed post-settlement mortality of echinoderms under field conditions (but see Andrew & Choat 1985, Rowley 1990, Sewell & Watson 1993, Ling & Johnson 2012). Keesing et al. (2018) demonstrated the effect of predation on small post-settlement juveniles of *Acanthaster cf. solaris* in a caging experiment and developed a model of size- and age-dependent mortality to calculate a settlement rate threshold that leads to destructive population irruptions of this corallivorous asteroid. Quantitative estimates of both settlement rates and early post-settlement mortality may not only improve our understanding of the supply-side ecology of echinoderms (*sensu* Lewin 1986), but also help resolve priority research questions pertaining to these processes in ecologically or economically important species.

Settlement behaviour

Many echinoderm larvae that are competent to settle and metamorphose respond to chemical cues indicating the suitability of a substratum and environment for their benthic life-history stage. Chemical settlement cues originate from a wide range of sources, and their characterisation appears critical to our understanding of spatiotemporal settlement patterns, and thus the supply-side ecology of echinoderm taxa (Hadfield & Paul 2001). Moreover, identifying mechanisms of induction has applicability in the successful and efficient settlement of echinoderms in aquaculture settings (reviewed by Hodin et al. 2019). Chemical cues identified to induce echinoderm settlement generally fall under one of four categories: gregarious cues, associative cues (e.g. prey), biofilm-associated cues and neurotransmitter or ion-associated cues (Tables 1 and 2). These cues, associated with various biotic sources, can be surface bound or waterborne cues and may thus act before the substratum is physically contacted by the larva or once this contact has been established (Figure 1). Initially, only surface-bound, non-polar settlement cues were considered capable of inducing larval settlement (Pawlik 1992), because the inductive effectiveness of waterborne cues was assumed to be hindered by rapid dilution and dispersion in the surrounding seawater, inhibiting larvae from reaching the appropriate substratum (Chia et al. 1984). More recently, numerous studies have shown that water-soluble cues associated with conspecifics or live substrata can function as *in situ* inducers of larval settlement and metamorphosis in echinoderms (e.g. Williamson et al. 2000, Swanson et al. 2004, Dworjanyan & Pirozzi 2008). In most echinoderms, a single inducer is expected to trigger the entire settlement process, including the initial substratum attachment and larval metamorphosis (e.g. Burke 1984, Pearce & Scheibling 1990b). However, in cases where the inductive compound has not been fully characterised, or only conditioned water treatments have been demonstrated to induce both settlement and metamorphosis, multiple chemical compounds may be present and affecting the two processes (Hadfield & Paul 2001).

Echinoid larvae settle readily in response to a wide range of natural chemical cues, including conspecifics, seagrasses, fleshy and coralline algae, and biofilms (Table 1). Echinoid larvae often respond to a suite of cues as opposed to a single chemical signal. With the exception of a few species known to respond to cues associated with conspecifics (Highsmith 1982, Highsmith & Emlet 1986), chemical cue specificity is relatively low in echinoids. Likewise, chemical cues appear to be required for the induction of settlement and metamorphosis in asteroids, although this has only been demonstrated for few asteroid species of ecological importance (Birkeland et al. 1971, Barker 1977, Johnson et al. 1991, Johnson & Sutton 1994). In these studies, asteroids exhibited associative settlement in response to cues associated with polychaetes (Birkeland et al. 1971, Bryan 2004) and coralline algae with bacterial films (Johnson et al. 1991, Johnson & Sutton 1994). Few studies have examined possible settlement and metamorphic cues in holothuroids, ophiuroids and crinoids; however, some species of these echinoderm classes appear to exhibit gregarious settlement (Table 1). Holothuroids will settle without stimulation, but the presence of periphytic diatoms (Ito & Kitamura 1997, Agudo 2007), seagrass (Mercier et al. 2000) and macroalgal surfaces (Agudo 2007) can increase settlement and metamorphic success. More so than other echinoderms, competent ophiuroid larvae metamorphose spontaneously in the plankton and settle naturally in the absence of specific exogenous cues (Hendler 1991, Selvakumaraswamy & Byrne 2006, Hodin et al. 2019).

Gregarious settlement

Gregarious settlement, the settlement of larvae in response to cues from conspecific individuals, has been well documented in many benthic marine invertebrates (reviewed by Burke 1986). Sessile marine benthic invertebrates demonstrating chemically specific gregarious settlement have been studied extensively, and many of the chemical cues they respond to have been fully or partially characterised (Pawlik 1992, Hadfield & Paul 2001). Although the vast majority of echinoderms are motile, their locomotory capacities are often limited to relatively small spatial scales and some species are even considered effectively sessile (Young & Chia 1982). Gregarious settlement can thus be of high ecological importance. The presence of conspecifics likely indicates species-specific habitat suitability, and may support post-settlement growth and survival due to prey availability, and suitable environmental conditions (Slattery 1997). In addition, population aggregations can potentially reduce mortality rates via predator swamping (Highsmith 1982, McCallum 1987) and enhance fertilisation rates and reproductive success (Crisp 1979, Babcock et al. 1994). At the same time, conspecific aggregations could increase competition for resources, especially for species with narrow ecological niches (Crisp 1979, Slattery 1997). Settlement and metamorphosis in response to conspecifics has been demonstrated in all classes of echinoderms except asteroids (Table 1). In contrast to many sessile marine invertebrate taxa, the specific chemical stimuli triggering these responses in echinoderms have not been characterised, with the exception of one irregular echinoid (Highsmith 1982, Burke 1984).

Larvae of the sand dollar *Dendraster excentricus* preferentially settled and metamorphosed on sand from beds of adult conspecifics (Highsmith 1982, Burke 1984, Highsmith & Emlet 1986). The chemical cue produced by adults, which was extracted from sand that has been isolated for 7 weeks, effectively induced metamorphosis in *D. excentricus* (Highsmith 1982). Larval settlement responses to sand treated with proteolytic enzymes and sand in dialysis tubing indicated that the responsible chemical cue is a small peptide with low molecular mass (Highsmith 1982). This characterisation was confirmed by Burke (1984), who isolated a purified 980 Da peptide that induced metamorphosis from sand extracts using both gel permeation and liquid chromatography. However, even for purified inducers like this peptide, we do not have any information about its amino acid composition and structure, and thus the reason for its specificity in settlement response is unclear. Peptide pheromone signalling may be driving the settlement in response to substrata or water conditioned with conspecifics in other irregular (Pearce & Scheibling 1990a, Takeda 2008) or regular

echinoids (e.g. Dworjanyn & Pirozzi 2008), but their chemical inducers have yet to be characterised. The sand dollar *Scaphechinus mirabilis* metamorphosed faster in adult-conditioned sand (Takeda 2008). Likewise, larvae of the sand dollar *Echinarachnius parma* showed a comparably high responsiveness to a water-soluble cue associated with sand conditioned with adult conspecifics in aquaria (Highsmith & Emllet 1986, Pearce & Scheibling 1990a). In the field, such specialised responses likely result in strongly preferential settlement of larvae in or near established sand dollar beds, demonstrating that settlement can occur onto populations of motile echinoderms that live in dense aggregations (Burke 1984). Small proportions of larvae of *E. parma* and *Dendraster excentricus* settled on non-conditioned substrata (Highsmith 1982, Burke 1984, Pearce & Scheibling 1990a) and newly settled *D. excentricus* have been observed outside of adult sand dollar beds in the field (Cameron and Rumrill 1982). Unlike in some sessile species (Nelson 1979), adult aggregations of these species can therefore not entirely be attributed to gregarious settlement of their larvae. However, the gregarious settlement of *D. excentricus*, *Scaphechinus mirabilis* and *Echinarachnius parma* is generally assumed to be contributing to an aggregated pattern in the distribution of adult populations.

In general, cue specificity is not high in echinoid settlement (Chia et al. 1984), and the sand dollar species mentioned above are assumed to be an exception to this rule. Accordingly, no evidence of gregarious settlement was found for the echinoid *Heliocidaris erythrogramma* (Huggett et al. 2006). Likewise, adult urchins, adult-conditioned seawater, their faecal matter and conspecific settlers did not induce larval metamorphosis in the echinoid *Strongylocentrotus droebachiensis* (Pearce & Scheibling 1991). A regular echinoid, *Tripneustes gratilla*, has been induced to settle in response to conspecific chemical cues (Dworjanyn & Pirozzi 2008). Larvae settled at high rates in the presence of conspecific juveniles and their faeces. Settlement of this echinoid, however, was also readily induced by cues associated with numerous types of seagrass, algae, coralline algae and, specifically, bacterial biofilms (Dworjanyn & Pirozzi 2008). These results were corroborated in a second study, which reported settlement induction of *T. gratilla* larvae by adult conspecifics, however, at significantly lower rates than in response to macroalgal cues (Mos et al. 2011). This suggests that even echinoid species found to be highly responsive to conspecific cues probably settle in response to a wide range of biotic chemical cues in nature.

Evidence of gregarious settlement in holothuroids, crinoids, ophiuroids and asteroids is highly fragmented. Competent larvae of the holothuroid *Psolus chitonoides* preferred to settle in response to conspecifics in experimental studies (Young & Chia 1982). Field experiments reporting high settlement either directly on top or around the sole of conspecific adults substantiated the hypothesis of gregarious settlement in this holothuroid (Young & Chia 1982). Likewise, larval crinoids settling gregariously in culture (Mladenov & Chia 1983, Obuchi et al. 2010) are supported by reports of crinoid settlers found on top or associated with the cirri of conspecific adults (Mladenov & Chia 1983), suggesting that gregarious settlement in crinoids may be a common and overlooked phenomenon. Preferential settlement in the proximity of conspecific adults has also been reported in the ophiuroid *Ophiothrix fragilis* (Warner 1971, Morgan & Jangoux 2004, 2005). Larval metamorphosis in ophiuroids begins spontaneously in the plankton; however, the presence of adult conspecifics clearly enhances the loss of two posterolateral rods and larval settlement (Morgan & Jangoux 2005). The loss of their posterolateral rods near a brittle star bed increases the likelihood of larvae settling in a suitable habitat (Morgan & Jangoux 2005), and hooked spines on settlers without their posterolateral rods may help them cling directly onto adults (Morgan & Jangoux 2004). However, in cases where the habitat or dietary requirements of settlers and conspecific adults differ, larval echinoderms may instead settle in response to chemical cues associated with prey or substratum they require during their early post-settlement stage. In the case of motile echinoderms, these juveniles may later migrate into habitat utilised by conspecific adults. For example, larvae of the asteroid *Mediaster aequalis* settled in response to tubes of a polychaete worm that juveniles were frequently observed on, while the presence of juvenile *M. aequalis* failed to trigger a settlement response (Birkeland et al. 1971). Spines and tube feet of conspecifics did not affect settlement rates in larvae of *Acanthaster* cf.

solaris (Henderson & Lucas 1971), although analyses of settlement preferences based on static choice chambers suggest that larvae may be attracted to adult conspecifics (Cowan et al. 2016b).

Associative settlement

Associative settlement, or settlement onto heterospecific plant or animal species (Crisp 1974), is seemingly widespread among echinoderms. Associative settlement can be broadly categorised based on predatory, herbivorous, parasitic and other non-parasitic associations between species (Pawlik 1992). In the case of echinoderms, this phenomenon most commonly refers to species responding to chemical cues associated with suitable habitat (Williamson et al. 2000, Ling et al. 2019) and potential prey species of herbivorous juveniles or adults (Rowley 1989, Pearce & Scheibling 1990b, 1991, Johnson et al. 1991).

Numerous species of echinoids, asteroids and holothurians have been found to settle and metamorphose in response to seagrass, coralline red algae, and red, green and brown fleshy algae (Table 1). However, the relative capacity of these substrata to induce settlement in echinoderm larvae varies greatly. For example, studies testing for differential settlement rates of echinoids in response to these substratum types reported that species of coralline red algae and red macroalgae generally induced the highest percentage of larval settlement, while the inductive capacity of brown algae, green algae and seagrasses was relatively low (Pearce & Scheibling 1991, Dworjanyn & Pirozzi 2008, Swanson et al. 2012). Moreover, chemical cue specificity is highly variable within and among echinoderm classes (Table 1). The echinoid *Tripneustes gratilla* was induced to settle by all 11 macroalgae tested including 6 brown algae, 1 green algae, 2 red algae and 3 coralline algae (Dworjanyn & Pirozzi 2008). In contrast, settlement in the asteroid *Mediaster aequalis* is induced predominantly by a specific chemical cue associated with the polychaete *Phyllochaetopterus prolifica* (Birkeland et al. 1971, Bryan 2004). In many cases, differences in the inductive capacity of natural substrata, as well as cue specificity of settlers, are likely linked to the presence or absence of specific chemical compounds in these substrata or animal prey. Purified compounds that induce associative settlement in echinoids have been isolated from red algae (Williamson et al. 2000, Swanson et al. 2004, 2006, 2012), coralline red algae (Kitamura et al. 1993, 1994) and endophytic microalgae (Taniguchi et al. 1994, Takahashi et al. 2002).

Naturally occurring settlement cues associated with red algae have been demonstrated for several ecologically important echinoid species (Rowley 1989, Pearce & Scheibling 1991, Williamson et al. 2000, Dworjanyn & Pirozzi 2008, Privitera et al. 2011), and chemical constituents of red algae that induce settlement and metamorphosis have recently been identified (Swanson et al. 2004, 2006, 2012). Newly settled echinoids of the species *Holopneustes purpurascens* are predominantly found on the red algae *Delisea pulchra* (Williamson et al. 2000, Swanson et al. 2006), although adult densities in the canopy of *D. pulchra* and the brown algae *Ecklonia radiata* are similar (Williamson et al. 2000). This pattern is hypothesised to be a response to a chemical cue produced by *Delisea pulchra*, as competent *Holopneustes purpurascens* larvae metamorphosed to cues associated with *Delisea pulchra*, but not the brown algae *Ecklonia radiata* (Williamson et al. 2000). The metamorphic cue was isolated and characterised by nuclear magnetic resonance spectroscopy as a water-soluble floridoside-isethionic acid complex (Williamson et al. 2000). Swanson et al. (2004) corrected this finding and identified the chemical identity of this cue produced by *Delisea pulchra* as histamine, by isolating the cue from the polar extract via cation-exchange chromatography. Corroborating this characterisation, the histamine content found in *D. pulchra* was reported to be one or more orders of magnitude higher than in the brown algae *Ecklonia radiata* and four other common species of fleshy and coralline algae (Swanson et al. 2004). Histamine exposure also appears to modulate metamorphic competence in other echinoids (Sutherby et al. 2012). With the first quantitative *in situ* measurements of a natural settlement cue in the habitat of a marine organism, Swanson et al. (2006) showed that seawater surrounding *Delisea pulchra* contained far higher

concentrations of histamine than for all other fleshy and coralline algae tested. The effectiveness of histamine as a metamorphic cue was demonstrated further for the lecithotrophic larvae of the echinoids *Holopneustes inflatus* and *Heliocidaris erythrogramma*, and the planktotrophic larvae of *Centrostephanus rodgersii* (Swanson et al. 2012). Conversely, histamine had a weak or no inductive effect on larvae of *Heliocidaris tuberculata* and *Tripneustes gratilla* (Swanson et al. 2012). A lower specificity in the metamorphic cues of these two habitat-generalist herbivores may be due to a relatively low restriction in their habitat and prey selection as juveniles and adults (Swanson et al. 2012). In contrast, dissolved histamine that originates from red algae on other plants likely serves as an exogenous cue for competent larvae of more habitat-specialised species such as *Holopneustes purpurascens* and *H. inflatus*, signalling the presence of a suitable habitat in which to settle (Swanson et al. 2012). Cues associated with histamine certainly have a role in settlement and metamorphic processes of echinoderms, which may extend past this group of ecologically important echinoids.

Settlement and metamorphic responses to natural chemical cues in other echinoids and asteroids have been described for numerous species of coralline red algae (Table 1). Both articulate and encrusting assemblages of coralline red algae may be comparably or even more inductive to some larvae than fleshy red macroalgae (Dworjanyn et al. 2008, Swanson et al. 2012). For example, encrusting coralline species of the genus *Lithothamnion* induce settlement and metamorphosis in competent *Acanthaster* cf. *solaris* larvae (Johnson et al. 1991, Johnson & Sutton 1994), and the echinoids *Strongylocentrotus purpuratus* (Rowley 1989) and *S. droebachiensis* (Pearce & Scheibling 1990b, 1991). Similarly, many echinoid species settle and metamorphose in response to cues associated with the articulated corallines *Amphiroa anceps* (Williamson et al. 2000, Swanson et al. 2006, 2012, Dworjanyn & Pirozzi 2008) and *Corallina* spp. (Lamare & Barker 2001, Pearce & Scheibling 1990b, 1991, Kitamura et al. 1992, Mos et al. 2011). Purified compounds responsible for the induction of settlement and metamorphosis in two commercially important echinoid species, *Pseudocentrotus depressus* and *Anthocidaris crassispina*, have previously been characterised from lipophilic extracts of the coralline red alga *Corallina pilulifera* (Kitamura et al. 1992, 1993, 1994). Silica gel column chromatography demonstrated that simple lipids including free fatty acids were the inducers of this settlement response (Kitamura et al. 1992). Further chemical analyses of a mixture of free fatty acids detected in *C. pilulifera* revealed that larvae of both echinoids only underwent settlement and metamorphosis in response to eicosapentaenoic acid and arachidonic acid (Kitamura et al. 1993). Responses of both echinoid larvae to a wide range of saturated and unsaturated fatty acids were highly specific and suggested that only highly unsaturated fatty acids (dihomo- γ -linolenic acid and eicosatrienoic acid) triggered strong metamorphic larval responses (Kitamura et al. 1994), which appears to be a similar induction mechanism for other motile marine invertebrates (Pawlik & Faulkner 1986).

Different chemical compounds isolated from extracts of the endophytic green microalgae *Ulvelia lens* have been identified to induce larval settlement and metamorphosis in the echinoids *Strongylocentrotus nudus* (Taniguchi et al. 1994, Takahashi et al. 2002) and *S. intermedius* (Takahashi et al. 2002). The compound dibromomethane, which was found in seawater in which *Ulvelia lens* and three coralline algae species were cultured, is the principal inducer of settlement and metamorphic responses in *Strongylocentrotus nudus* (Taniguchi et al. 1994). Further investigating chemical cues associated with *Ulvelia lens*, Takahashi et al. (2002) reported that settlement and metamorphic responses of *Strongylocentrotus nudus* and *S. intermedius* were only triggered by relatively high concentrations of dibromomethane, and a polyunsaturated fatty acid (eicosapentaenoic acid) did not induce settlement at all. Instead, several active compounds isolated from *Ulvelia lens* extracts were identified as glycolipids (Takahashi et al. 2002), which are a class of cell wall-associated compounds abundant in marine algae (Tebben et al. 2015). These findings underline the importance of assessing taxa-specific inducers to gain an accurate understanding of the chemical cues driving the mechanisms and patterns of larval settlement in echinoderms.

Biofilm-induced settlement

Biofilms are complex and dense consortia of microorganisms, which accumulate on the surfaces of most marine substrata (Dobretsov 2010). Marine biofilms usually consist of various species of bacteria, *Archaea* and unicellular organisms such as diatoms (Rahim & Kitamura 2004, Dobretsov 2010) and commonly include secreted extracellular substances in which the cells of these component organisms are situated (Hadfield 2011). The reasons why competent larvae choose to settle on biofilms are not always clear. Biofilms may be a possible food source for some newly settled echinoderms (de la Uz et al. 2013), while in some cases, settlement is thought to occur in response to cues simply signalling the presence of a nontoxic surface, which accumulated a biofilm and microorganisms over time (Hadfield 2011). Most research on biofilm-induced settlement in echinoderms has focused on cues associated with biofilm bacteria (Table 1); however, echinoderm larvae have also been induced to settle by various diatoms (Ito & Kitamura 1997, Rahim & Kitamura 2004, Agudo 2007, Mos et al. 2011), which are single-celled algae commonly found in marine biofilm assemblages (Dobretsov 2010). Among echinoderm classes, the inductive capacities of marine biofilm consortia have been demonstrated in echinoids (e.g. Lamare & Barker 2001, Rahim & Kitamura 2004), asteroids (e.g. Barker 1977, Johnson & Sutton 1994) and holothuroids (e.g. Ito & Kitamura 1997).

Early reports of settlement induction in echinoderms by marine biofilms (e.g. Cameron & Hinegardner 1974, Barker 1977) have raised the question whether many of the natural chemical cues of echinoderm settlement attributed to marine algae and other live substrata may, in fact, be produced by marine bacteria and unicellular eukaryotes on the surfaces of these substrata. Differential inductive capacity of naturally occurring algal substrata with and without biofilms, as well as isolated cues from the biofilms and their compounds, has been investigated for echinoderm larvae (Pearce & Scheibling 1990b, Johnson et al. 1991, Johnson & Sutton 1994, Swanson et al. 2006, Dworjanyn & Pirozzi 2008, Mos et al. 2011). It appears that in some cases, only the biofilm is required to induce settlement (Swanson et al. 2006, Dworjanyn & Pirozzi 2008), while others demonstrated that the algal substratum, but not the biofilm (Pearce & Scheibling 1990b), or both (Johnson & Sutton 1994) were essential to produce the inductive response.

Antibacterial treatment of the coralline red algae *Amphiroa anceps* substantially reduced larval settlement rates of the echinoid *Holopneustes purpurascens* (Swanson et al. 2006). Here, a settlement cue from the coralline algae is proposed to be bacteria-derived histamine, which is released into the surrounding seawater. Two isolated bacterial strains, *Photobacterium phosphoreum* and *Thalassomonas viridans*, cultured from the surfaces of the corallines induced settlement and contained histamine, while no histamine was detected in coralline extracts (Swanson et al. 2006). Further supporting the hypothesis of Steinberg et al. (2001) that generalist herbivorous echinoids metamorphose in response to biofilms, Dworjanyn & Pirozzi (2008) demonstrated the necessity of bacterial film growing on algal surfaces in producing an inductive compound. The removal of bacteria from the surface of three macroalgae significantly inhibited settlement of *Tripneustes gratilla* larvae in response to these macroalgae (Dworjanyn & Pirozzi 2008), which demonstrates the larvae did not respond to cues originating from the algae per se. The echinoid *T. gratilla* appears to have very little specificity in its settlement cues and likely settles on a wide range of surfaces with bacterial films present. Conversely, larvae of the same echinoid species were induced to settle at substantially higher rates by the addition of macroalgae-conditioned seawater to biofilm treatments (Mos et al. 2011), which indicates that compounds associated with the alga itself may at least contribute to settlement induction. Bacteria-derived settlement cues as inducers of echinoid settlement were also not supported by Pearce & Scheibling (1990b). Here, antibiotic treatment of the coralline red algae *Lithothamnion glaciale* and subsequent reduction of surface bacteria by two orders of magnitude did not affect the capacity of *L. glaciale* to induce metamorphosis in the echinoid *Strongylocentrotus droebachiensis* (Pearce & Scheibling 1990b).

Substratum selectivity by crown-of-thorns starfish (*Acanthaster cf. solaris*) also appears to be mediated by chemical cues produced by epiphytic bacteria (Johnson et al. 1991, Johnson & Sutton 1994). Larval settlement and metamorphosis of this asteroid is inhibited in the absence of bacteria on highly inductive shards of the coralline alga *Lithothamnium pseudosorum* (likely *Lithothamnion proliferum*), with settlement rates reduced to low levels when the coralline alga was treated with antibiotics (Johnson et al. 1991). Likewise, Yamaguchi (1973) reported that larval settlement of *Acanthaster cf. solaris* was not induced by bleached coralline algae. Moreover, settlers of this asteroid were only observed in sections of the coralline algal substratum with high densities of epiphytic bacteria, but not on the sections with little or no bacterial film cover (Johnson et al. 1991, Johnson & Sutton 1994). However, when isolated from soluble algal compounds, surface bacteria failed to induce settlement in *Acanthaster cf. solaris* larvae (Johnson & Sutton 1994). This demonstrates that either chemical compounds from both the coralline algae and the bacteria are essential to induce settlement and metamorphosis, or, more likely, the bacteria require the substratum from the alga to produce the inductive compound (Johnson & Sutton 1994).

Among a range of other marine bacteria identified to induce echinoderm settlement (Table 1), the bacterial genus *Pseudoalteromonas*, and especially the bacterium *P. luteoviolacea*, has been recognised as strongly inductive and important to biofilm-associated settlement (Hadfield 2011). Huggett et al. (2006) isolated 250 bacterial strains from coralline algae and tested their capacity to induce settlement in the echinoid *Heliocidaris erythrogramma*. Many strains of bacteria induced substantially higher settlement rates than the corallines, and *Pseudoalteromonas* dominated highly inductive strains (Huggett et al. 2006). This culture-based result was supported by an assessment of larval responses to characterised biofilms in the field, which reported the highest metamorphic rates for the highly inductive *P. luteoviolacea* (Huggett et al. 2006). Other bacterial genera represented in highly inductive strains were *Photobacterium*, *Shewanella* and *Vibrio*; however, the same genera were also abundant in low inducers (Huggett et al. 2006). This indicates that the inductive capacity of marine bacteria is species-specific, and the settlement response of echinoderm larvae to bacterial films is likely determined by its specific bacterial composition. Altogether, this body of research suggests that the role of biofilms as cues in the settlement behaviour and metamorphosis of echinoderm larvae may be much more complex and widespread than previously suspected and certainly warrants further research.

Neurotransmitter and ion-induced settlement

Aside from the natural chemical cues associated with conspecifics, prey species and biofilms, various ‘artificial’ compounds have been identified to trigger larval settlement in echinoderms (Table 2). These inducers mimic natural chemical compounds and include numerous neurotransmitters (e.g. dopamine), neurotransmitter precursors (e.g. L-DOPA) and ions (e.g. potassium), which corroborates the role of neuronal receptors in initiating a settlement response (Rodriguez et al. 1993). Although these neuroactive compounds and ions may not always act as predominant cues of settlement in nature, their study furthers our understanding of chemoreception, neural control and the mechanisms driving larval response (Slattery 1997). Investigating and understanding their effects is of considerable interest, particularly their potential to improve settlement success and survival rates in echinoderm aquaculture (Slattery 1997, Nontunha et al. 2021).

Amino acid derivatives

Several amino acid derivatives have been shown to effectively induce settlement and metamorphosis in echinoderms, including glutamine (Yazaki & Harashima 1994, Naidenko 1996), gamma aminobutyric acid (GABA; Pearce & Scheibling 1991, Rahman & Uehara 2001, Bryan 2004, Sun et al. 2014, Nontunha et al. 2021), glutamic acid (Naidenko 1996) and monosodium glutamate (Nontunha et al. 2021). Glutamine is an essential amino acid and the precursor of GABA, an inhibitory neurotransmitter. Levels of GABA are enhanced by glutamic acid, which, in turn, is often

used in the form of its sodium salt, monosodium glutamate (Nontunha et al. 2021). Induction of metamorphosis by glutamine has been observed in the echinoid species *Pseudocentrotus depressus* (Yazaki & Harashima 1994), *Scaphechinus mirabilis* and *Strongylocentrotus intermedius* (Naidenko 1996). Glutamic acid was also shown to induce metamorphosis in some echinoid species (*Scaphechinus mirabilis* and *Strongylocentrotus intermedius*; Naidenko 1996), but not all (*Pseudocentrotus depressus*; Yazaki & Harashima 1994), and had a toxic effect on *Scaphechinus mirabilis* and *Strongylocentrotus intermedius*, which was possibly caused by a decrease in seawater pH from 8.4 to 7.5 at a glutamic acid concentration of 100 µg/mL (Naidenko 1996). Monosodium glutamate (MSG), a glutamic acid derivative, induced larvae of the holothuroid *Holothuria scabra* to settle at high rates, and MSG was also shown to be the least toxic in comparison with other neurotransmitters tested (Nontunha et al. 2021). Another neuroactive compound, serotonin, which is a derivative of tryptophan, failed to trigger any settlement and metamorphosis response in the Japanese holothuroid *Apostichopus japonicus* (Sun et al. 2014, Matsuura et al. 2009) and the Pacific sand dollar *Dendraster excentricus* (Burke 1983b).

GABA is an inhibitory neurotransmitter, which can produce depolarisation of cells capable of activating metamorphosis (Baloun & Morse 1984). Induction by this endogenous chemical cue is known to occur in a wide range of benthic marine invertebrates (Slattery 1997) and has thus been extensively tested for numerous echinoids, asteroids and holothuroids (Table 2), although results are variable both among and within echinoderm classes. Five echinoid species, including *Echinometra mathaei*, *E. oblonga* and *Strongylocentrotus droebachiensis*, have been found to metamorphose in response to GABA (Pearce & Scheibling 1990, Rahman & Uehara 2001). On the other hand, no effect at all was observed in *Dendraster excentricus* (Burke 1983b) and the echinoid *Pseudocentrotus depressus* (Yazaki & Harashima 1994). Likewise, bioassays with GABA induced settlement and metamorphosis in larvae of the asteroid *Mediaster aequalis* (Bryan 2004), but not the crown-of-thorns starfish, *Acanthaster cf. solaris* (Johnson et al. 1991). Holothurians have successfully been induced by a wide range of neurotransmitters (Table 2), including GABA (Sun et al. 2014, Nontunha et al. 2021). GABA induced high rates of settlement in *Holothuria scabra* larvae, while a pair of studies found this compound to trigger larval settlement behaviour (Sun et al. 2014), but not metamorphosis (Yazaki & Harashima 1994) in *Apostichopus japonicus*. The highly variable results encountered in the response of echinoderm larvae to GABA may explain why this neurotransmitter has not been generally used as an inducer of settlement and metamorphosis in the aquaculture of commercially important echinoderm taxa.

Tyrosine derivatives

Catecholamines (dopamine, epinephrine and norepinephrine) and their precursor levodopa (L-DOPA) are tyrosine derivatives with numerous biological functions, such as structural proteins, hormones and neurotransmitters. As in many other marine benthic invertebrates, these tyrosine derivatives are reliable inducers of larval settlement in echinoderms (Table 2). Epinephrine and norepinephrine are similar tyrosine derivatives that act as neurotransmitters and hormones. Epinephrine has been shown to initiate metamorphosis, but not settlement, in the Japanese holothuroid *Apostichopus japonicus*, while norepinephrine initiates both settlement behaviour and metamorphosis (Matsuura et al. 2009, Sun et al. 2014). Conversely, neither compound was found to be an effective inducer of larval metamorphosis in the echinoid *Dendraster excentricus* (Burke 1983b). Dopamine and L-DOPA, which increases dopamine neurotransmission, have been identified as the most efficient chemical cues to induce settlement of *Apostichopus japonicus* (Matsuura et al. 2009, Sun et al. 2014), *Holothuria scabra* (Nontunha et al. 2021) and the sand dollar *Dendraster excentricus* (Burke 1983b). These findings suggest that dopamine acts as the chemical transmitter during settlement induction in various echinoderm taxa. This endogenous chemical cue is thought to either directly stimulate larval tissues containing the effectors of metamorphosis, or indirectly trigger it by inducing the release of substances stimulating these tissues (Burke 1983b). The interference and

inhibition of metamorphosis by reserpine (Burke 1983b), a compound known to deplete catecholamines, further supports this conclusion.

Choline derivatives

The neurotransmitter acetylcholine is the sole choline derivative documented to induce effective larval settlement in an echinoderm, the holothuroid *Apostichopus japonicus* (Sun et al. 2014). This neuroactive compound, however, failed to induce larval metamorphosis in the sand dollar *Dendraster excentricus* (Burke 1983b). Choline, a precursor to acetylcholine, is a bound constituent of membranes surrounding cells. In contrast to acetylcholine, this compound had no significant inductive effect on *Apostichopus japonicus* larvae (Sun et al. 2014); however, it has been suggested to have an indirect effect on holothuroid settlement by participating as precursors in acetylcholine biosynthesis rather than by acting directly on the cholinergic receptors (Rodriguez et al. 1993). Similar to some catecholamine derivatives, choline derivatives are thus generally unlikely to directly induce echinoderm settlement and metamorphosis in nature by acting directly on cholinergic receptors, but instead more likely act as precursors in the synthesis and release of neurotransmitters (Hirata & Hadfield 1986, Slattery 1997).

Ions

In addition to neurotransmitters and their precursors, some ions can stimulate larval settlement in echinoderms (Table 2). The sensory bases of induction indicate that the nervous system plays a significant role in the cascade of events comprising benthic marine invertebrate settlement and metamorphosis (Burke 1983b). The successful transmission of neural signals relies on the electrical potential across cell membranes, which, in turn, is affected by the permeability of these membranes to ions (Rodriguez et al. 1993). Hence, any ions or compounds that affect ionic transport through cell membranes can trigger inductive responses, and their potential effects on echinoderm larvae should be assessed.

The highly inductive effects of potassium ions (K^+) on echinoderm settlement have been documented, particularly for echinoids (Table 2). At least 15 echinoid species from seven families have been induced to settle and metamorphose at variable potassium chloride concentrations within 1 hour of exposure (Hodin et al. 2019). More broadly, the inductive effects of potassium have also been observed in the holothuroid *Apostichopus japonicus* (Sun et al. 2014). Increased exogenous K^+ likely activates settlement responses through a depolarisation of externally accessible cells, which are directly involved in the recognition of natural inducers (Yool et al. 1986). Tetraethyl ammonium, a compound that selectively occludes potassium channels, inhibits metamorphosis (Rodriguez et al. 1993), which suggests that potassium could act through this channel in echinoderm larvae. Conversely, no settlement was induced by high concentrations of potassium in larvae of the crown-of-thorns starfish *Acanthaster cf. solaris* (Johnson et al. 1991).

Other ions that may trigger settlement and metamorphosis in echinoderms are calcium (Ca^{2+}), ammonium (NH_4^+) and magnesium (Mg^{2+}). Calcium has been implicated in the transmission or modulation of signals in the echinoid *Lytechinus variegatus* (Cameron et al. 1989) and other marine invertebrate larvae (Yool et al. 1986, Yu et al. 2008). Sun et al. (2014) reported inductive effects of Ca^{2+} on the settlement behaviour of *Apostichopus japonicus* larvae; however, no obvious effect on settlement success was found. Larvae of this holothuroid have also been induced to settle in response to ammonium ions (NH_4^+), although ammonium was concluded to be a relatively ineffective inducer in comparison with potassium (Sun et al. 2014). Magnesium ions appear to have no effect on *A. japonicus* larvae (Sun et al. 2014), which corroborates previous conclusions in other benthic marine invertebrates (Baloun & Morse 1984, Yool et al. 1986). Conversely, an inhibitory effect of Mg^{2+} was documented in the echinoid *Lytechinus variegatus*

(Cameron et al. 1989). Here, excess magnesium interferes with echinoid metamorphosis in the presence of inductive biofilms by competing with Ca^{2+} for binding molecules involved with the release of neurotransmitters (Cameron et al. 1989). Similar inhibitory effects of magnesium may be found in *Apostichopus japonicus* or other echinoderm larvae if tested in the presence of metamorphically active biofilms.

Multiple lines of evidence support the notion that ionic fluxes play a role in the induction of larval settlement and metamorphosis (Cameron et al. 1989). Because of their inductive capacity, some of these ions, especially potassium, are more commonly utilised as agents in the cultivation of numerous benthic marine invertebrates, replacing the use of neurotransmitters such as GABA or L-DOPA (Rodriguez et al. 1993).

Sampling methods for the study of settlement patterns

A variety of sampling methods have been trialled and used to study echinoderm settlement patterns (Figure 4); however, there are no standard or established sampling techniques used among or even within echinoderm classes (Tables 3–6). The extremely small size and often cryptic nature of recently settled echinoderms has greatly constrained progress in the study of this important life-history stage in their natural environments. In the past, inter-annual settlement patterns of some species have commonly been inferred based on the distribution and abundance of juveniles or adults

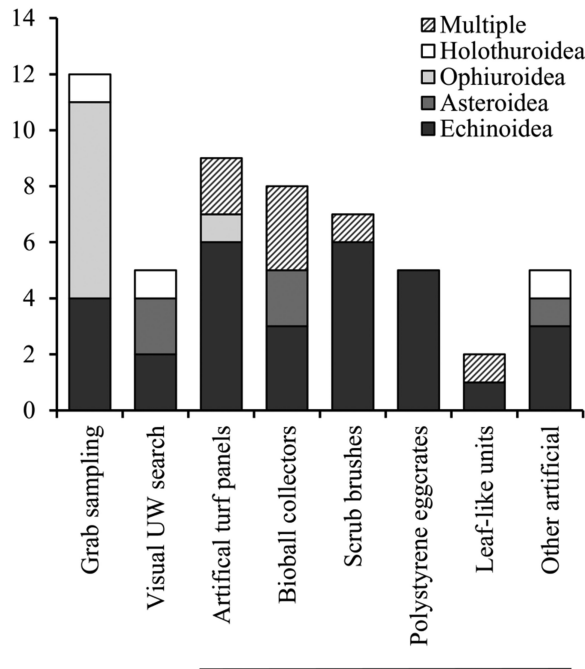


Figure 4 Frequency distribution of sampling methods used in 53 studies that assessed spatial and/or temporal patterns of larval settlement in one or multiple classes of echinoderms. The horizontal line indicates the sampling methods utilising artificial settlement collectors.

Table 3 Summary of studies assessing spatial and temporal settlement patterns in echinoids

Species	Location (climate)	Habitat; depth	Patterns observed	Sampling frequency; dates	Methodology	Reference
<i>Arbacia lixula</i>	Canary Islands, Spain (subtropical)	Four subtidal habitats: seagrass meadows, urchin barrens, macroalgal beds and sandy patches; 5–10 m	Settlement rates were relatively low and varied among seasons, as all newly settled echinoids were recorded between January and May.	Monthly, Feb 2009–Feb 2010	Plastic cushion-shaped leaf-like units	García-Sanz et al. (2014)
<i>Arbacia lixula</i>	Canary Islands, and Costa Brava, Spain (subtropical)	Gently sloping rocky barren bottom; 5–10 m	The plastic bioball collectors reported the highest settler densities. No settlers were found at the Mediterranean site (Costa Brava). At the eastern Atlantic site (Canary Is.), a considerably higher number of settlers was recorded in the collectors deployed for 28 days than in those deployed for 14 days.	Deployments in Feb (Canary Is.) and Jun 2012 (Costa Brava); two retrievals from both locations 14 and 28 days post-deployment	Plastic bioballs in nylon nets; vertical scrub brushes with vegetal bristles; horizontal triangular mats of coconut fibre	Balsalobre et al. (2016)
<i>Dendraster excentricus</i>	Monterey Bay, the USA (subtropical)	Inshore sand dollar bed; 8–15 m	Settlement occurred at all sampling times during the summer months of 1980, and settler densities were relatively constant throughout this time period.	Fortnightly; Jul–Oct 1980	Eckman grab samples and cylindrical cores	Cameron & Rumrill (1982)
<i>Diadema africanum</i>	Canary Islands, Spain (subtropical)	Rocky subtidal zone; 5–6 m	Substantial intra-annual variation in settlement observed at both sites. The primary peak between August and October may be related to spawning intensity (April–June), while a secondary peak in January/February suggests that factors other than spawning intensity may also be driving local settlement patterns.	Monthly (with exceptions); Apr 2002–Apr 2003	Plastic bioballs inside net bags	Hernández et al. (2006)
<i>Diadema africanum</i>	Canary Islands, Spain (subtropical)	Rocky subtidal zone; 5–10 m	Settlement was observed at all sites within three survey locations (MPA; fished; and heavily fished). The number of settlers found was similar between sites and locations, which suggests larval supply is unlikely to be limiting recruitment in any of the three locations.	Single deployment; Sep–Oct 2006	Plastic bioballs inside net bags	Clemente et al. (2009)

(Continued)

Table 3 (Continued) Summary of studies assessing spatial and temporal settlement patterns in echinoids

Species	Location (climate)	Habitat; depth	Patterns observed	Sampling frequency; dates	Methodology	Reference
<i>Diadema africanum</i>	Canary Islands, Spain (subtropical)	Urchin barrens, and macroalgal beds; 6–10 m	Single annual peak in settlement during August to October, which was consistent among years and locations; however, inter-annual variability in settlement was high at the Abades and Boca Cangrejo locations. Higher densities of settlers were found in the barren areas than in the macroalgal beds. Strong spatiotemporal settlement variability likely driven by temperature; however, settlement rates were also negatively correlated with food availability 2 months pre-settlement.	Monthly; Apr 2002–Apr 2008 (Abades), May 2002–Apr 2003 (Masca), Dec 2003–Apr 2008 (Boca Cangrejo) and Oct 2006 (El Hierro)	Plastic bioballs inside net bags	Hernández et al. (2010)
<i>Diadema africanum</i>	Canary Islands, Spain (subtropical)	Four subtidal habitats: seagrass meadows, urchin barrens, macroalgal beds and sandy patches; 5–10 m	Settlement followed a clear unimodal pattern with a main peak occurring in September and October and few newly settled echinoids observed in the months following. Densities were greater in urchin barrens and sandy patches than in the other habitats.	Monthly; Feb 2009–Feb 2010	Plastic cushion-shaped leaf-like units	García-Sanz et al. (2014)
<i>Diadema antillarum</i>	Curaçao, southern Caribbean Sea (tropical)	Coral reef; 8 m	Settlement occurred continuously and peaked in the spring and autumn months. Settlement rates were relatively similar among years, but differed between sites.	Fortnightly with exceptions; 1982–1984	Settlement plates consisting of two polystyrene egg crates and plexiglass in-between	Bak (1985)
<i>Diadema antillarum</i>	Barbados, eastern Caribbean Sea (tropical)	Coral reef	Low settlement was detected between June and August and peaked in July. Settlers were always found within the front third of the reef (offshore) on rugose substrata and aggregated with adults.	Monthly; Oct 1984–Dec 1985	Visual UW searches for settlers	Hume & Younglao (1988)
<i>Diadema antillarum</i>	Florida Keys, the USA (subtropical); Puerto Rico (tropical)	Variable habitats (fore reef, back reef, drowned reef and bank reef) and sampling depths; 3–19 m	While settlers were detected in low numbers at all locations, only one of the Puerto Rico sites recorded a substantial settlement pulse. These results corroborate the hypothesis of low larval supply (and settlement) limiting the recovery of this species in the Florida Keys.	Monthly; Aug 2005–Jul 2006 (Florida Keys), and Jun 2006–Oct 2006 (Puerto Rico)	Settlement plates consisting of two polystyrene egg crates and plexiglass in-between	Miller et al. (2009)

(Continued)

Table 3 (Continued) Summary of studies assessing spatial and temporal settlement patterns in echinoids

Species	Location (climate)	Habitat; depth	Patterns observed	Sampling frequency; dates	Methodology	Reference
<i>Diadema antillarum</i>	La Parguera, Puerto Rico (tropical)	Coral reef; 19–6 m (shelf-edge), 10–5 m (mid-shelf) and 2–3 m (inshore)	Substantially higher settlement at shelf-edge reef (275 recruits) compared to mid-shelf (two recruits) and inshore reefs (0 recruits). Unimodal settlement peak in July, with low settler densities from October to June. Settlement peaked in early June, similar to peaks in 1982 and 1983 (historic data comparison). Mean settlement rates in 2005 were > two times lower compared to pre- <i>D. antillarum</i> die-off numbers (1982–83), but substantially higher than those measured after the die-off (1984). No spatial variation among sites around the island.	Monthly; Sep 2005–Sep 2006	Artificial turf on horizontal and vertical plates	Williams et al. (2010)
<i>Diadema antillarum</i>	Curaçao, southern Caribbean Sea (tropical)	Coral reef; 3–5 m	Settlement peaked in early June, similar to peaks in 1982 and 1983 (historic data comparison). Mean settlement rates in 2005 were > two times lower compared to pre- <i>D. antillarum</i> die-off numbers (1982–83), but substantially higher than those measured after the die-off (1984). No spatial variation among sites around the island.	Fortnightly; Mar–Jul 2005	Settlement plates consisting of two polystyrene egg crates and Formica sheets in-between	Vermeij et al. (2010)
<i>Diadema antillarum</i>	La Parguera, Puerto Rico (tropical)	Coral reef; 3–17 m (depending on water depth)	Highest settlement at 9 m, intermediate at 6 and 12 m, and lowest at 3 and 15 m. Substantially higher settlement at two shelf-edge reefs (217 of 220 settlers), with little and no settlement detections at mid- and inner-shelf reefs. Settlement peaked in September, but was also relatively high in July.	Monthly; Feb–Apr and Jul–Sep 2008	Artificial turf on vertical plates	Williams et al. (2011)
<i>Diadema antillarum</i>	Curaçao, southern Caribbean Sea (tropical)	Variable habitats (fore reef, sheltered lagoon or back reef)	Settlement was variable in space. Significantly higher settlement rates were observed in sheltered habitats (lagoon and back reef) than in fore reef habitats.	Monthly; May/ Jun–Aug 2010	Settlement plates consisting of two polystyrene egg crates and plastic sheets in-between	Rogers & Lorenzen (2016)
<i>Diadema antillarum</i>	Xcalak, Mexico (tropical)	Coral reef lagoon and fore reef zone; <1, 2.5, 3 and 7 m	Sampled a total of five settlers during the 11-month period, all of which settled in the fore reef habitat at 7 m (4 in August and 1 in December).	Monthly; May 2014–Apr 2015	Settlement plates consisting of polystyrene egg crates and acrylic sheets in-between	Maldonado-Sánchez et al. (2019)

(Continued)

Table 3 (Continued) Summary of studies assessing spatial and temporal settlement patterns in echinoids

Species	Location (climate)	Habitat; depth	Patterns observed	Sampling frequency; dates	Methodology	Reference
<i>Evechinus chloroticus</i>	Hauraki Gulf, New Zealand (subtropical)	Urchin barrens & shallow mixed-algal assemblages; 4–5 m	No settlers were found at the sheltered, high-sediment location (Little Manly), while spatiotemporal variability in settlement was evident among sites and sampling months at the wave-exposed, low-sediment location (Leigh).	Nov 2003–Mar 2004	Underwater suction sampling and sieving	Walker (2007)
<i>Evechinus chloroticus</i>	Wellington region, New Zealand (temperate)	Rocky reef; 4–7 m	Highly variable settlement among sampling years and locations. Settlers were most abundant in 2019 at Shelly Bay, and smaller pulses of settlement occurred at Beaker Bay (2018, 2019) and Kau Bay (2018). Overall echinoderm settlement pulses were positively correlated with shell cover, seawater temperature and chlorophyll.	Annually; Nov 2016–Apr 2017; Nov 2017–Apr 2018; Dec 2018–Feb 2019	Plastic bioballs inside nylon nets	Glockner-Fagetti & Phillips (2020)
<i>Mesocentrotus franciscanus</i>	Northern & southern California, the USA (subtropical)	Not stated, but likely variable	Marked seasonality in settlement as most settlement occurred during one or multiple settlement pulses between February and July each year. Settlement was highly variable among years, and spatial settlement clusters did not form contiguous geographic subunits.	Weekly; Feb/Mar 1990–Jul 1993 at most sites, with shorter periods at others	Scrub brushes with nylon bristles	Ebert et al. (1994)
<i>Mesocentrotus franciscanus</i>	Southern Oregon, the USA (temperate)	18 m (Port Oxford) & 22 m (Gregory Point)	Settlement occurred from April to August at both locations. Settler densities were variable between locations and sampling years, but were most consistently high in June. Settlement pulses were stronger in 1995 and generally associated with warm water events characterised by a mixed water column and northward wind stress.	Deployments ranging from 9 to 35 days; Feb to Aug in 1994 and 1995	AstroTurf inside PVC pipe	Miller & Emlert (1997)
<i>Paracentrotus lividus</i>	Tossa de Mar, Spain (temperate)	Vertical wall occupied by seaweeds; 3, 6 and 9 m	Settler densities (<2 mm) varied substantially within and among years. Unimodal peaks in settlement were observed during the each of the four recruitment seasons (May–August), but peak densities were much higher in 1992 and 1995, compared to 1993 and 1994.	Fortnightly; Jun 1992–Jul 1993, Jun 1994–Dec 1995	Substrate collection using 20 × 20 cm ²	López et al. (1998)

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Table 3 (Continued) Summary of studies assessing spatial and temporal settlement patterns in echinoids

Species	Location (climate)	Habitat; depth	Patterns observed	Sampling frequency; dates	Methodology	Reference
<i>Paracentrotus lividus</i>	Medes Islands Marine Reserve, Spain (temperate)	Rocky bottoms colonised by a rich algal assemblage; 5, 10, 15 and 20 m	Reported single annual settlement peak within 3 weeks (May–June) and substantial inter-annual differences in settlement by more than two orders of magnitude. Preferential settlement at shallow depths (5 and 10 m). Spatial variation was found at all scales, and settlement was related to wave exposure and currents, but not to substratum type, level of protection and adult densities, suggesting physical processes may be driving these variable settlement patterns.	Weekly (spring–late summer) or every other week (rest of the year); Mar 1998–Oct 2000	Scrub brushes with vegetal bristles	Hereu et al. (2004)
<i>Paracentrotus lividus</i>	Medes Islands Marine Reserve, Spain (temperate)	Seagrass meadow, and vertical rock wall; 3, 5 (and 10 m at seagrass meadow only) in Apr 2000–July 2001; then 5 m only	Major settlement peak in April/May and minor peak in October/November. Inter-annual variability in settlement was high (~one order of magnitude). Settlement was generally higher in the vertical rock wall habitat than in the seagrass meadow.	Weekly or fortnightly (Apr 2000–Jul 2001); additional sampling in autumn–winter 2002 and early summer 2003	Scrub brushes with vegetal bristles	Tomas et al. (2004)
<i>Paracentrotus lividus</i>	Canary Islands, Spain (subtropical)	Four subtidal habitats: seagrass meadows, urchin barrens, macroalgal beds and sandy patches; 5–10 m	Densities of newly settled echinoids differed substantially among the four habitats surveyed, with collectors deployed in sandy patches reporting greater numbers than in the other habitats.	Single deployment for 4 weeks from early Aug to early Sep 2008	(A) Plastic leaf-like units; (B) cushion-shaped, leaf-like units; and (C) cushion-shaped units	García-Sanz et al. (2012)
<i>Paracentrotus lividus</i>	Canary Islands, Spain (subtropical)	Four subtidal habitats: seagrass meadows, urchin barrens, macroalgal beds and sandy patches; 5–10 m	Almost all newly settled echinoids were recorded during a main peak between February and April. During this peak, abundances of settlers differed substantially among the four habitats surveyed, with soft substrata (sandy patches and seagrass) reporting greater densities than hard substrata (barrens and macroalgal beds).	Monthly; Feb 2009–Feb 2010	Plastic cushion-shaped, leaf-like units	García-Sanz et al. (2014)

(Continued)

Table 3 (Continued) Summary of studies assessing spatial and temporal settlement patterns in echinoids

Species	Location (climate)	Habitat; depth	Patterns observed	Sampling frequency; dates	Methodology	Reference
<i>Strongylocentrotus droebachiensis</i>	Isles of Shoals, the USA (temperate)	Kelp beds and barren grounds; 0–30 m	Annual settlement pulses were substantial and settlement decreased with depth below 9 m.	Single deployments in Jun–Jul 1990, 1992 and 1993	Plastic turf	Harris et al. (1994)
<i>Strongylocentrotus droebachiensis</i>	Gulf of Maine, the USA; Bay of Fundy and Nova Scotia, Canada (temperate)	Kelp beds, silt and barren grounds; 5–30 m	Settlement in the Gulf of Maine was three orders of magnitude higher than in the Bay of Fundy and one order of magnitude higher than on Nova Scotia's Atlantic Coast. Spatial differences in settlement among sites within these regions were within the same order of magnitude. Settler densities were higher in barren grounds than in adjacent kelp beds.	Fortnightly to bi-monthly sampling intervals; May–Sep 1994	Plastic turf and scrub brushes	Balch et al. (1998)
<i>Strongylocentrotus droebachiensis</i>	Nova Scotia, Canada (temperate)	Kelp beds and urchin barren grounds; 5–10 m	Nearly all settlement occurred in July each year, but few settlers were reported up to October. Settlement was very low in 1992 and 1993, and the only major settlement occurred in early July 1994. Settlement rates were quite similar between kelp and barren sites.	Fortnightly; Jun–Nov 1992, May–Nov 1993 and Jun–Oct 1994	AstroTurf inside PVC pipe	Balch & Scheibling (2000)
<i>Strongylocentrotus droebachiensis</i>	Gulf of Maine, the USA (temperate)	7 m	Settlement peaked in mid-June, relatively high throughout June and early July, and low to absent from mid-July to early September. No differential settlement was reported during the peak in settlement among six substrate types deployed; however, settlers preferentially settled on coralline algae encrusted substratum during the remainder of the sampling period.	Weekly; 48-hour deployments in Jun–mid-Jul; 1-week deployments in late Jul–early Sep	AstroTurf plexiglass panels	Lambert & Harris (2000)
<i>Strongylocentrotus droebachiensis</i>	Bocabec Cove, Canada (temperate)	Rocky subtidal zone	Highly variable settlement among years, intra-annual sampling periods and sites. Highest density of settlers in mid-July 2005 at the site closest to the larger body of water, Passamaquoddy Bay. If transported to the area by currents, larvae would likely reach this site first and, if competent, settle.	Fortnightly; Jun–Oct 2004; Jun–Oct 2005	AstroTurf inside PVC pipe	Jennings & Hunt (2010)

(Continued)

Table 3 (Continued) Summary of studies assessing spatial and temporal settlement patterns in echinoids

Species	Location (climate)	Habitat; depth	Patterns observed	Sampling frequency; dates	Methodology	Reference
<i>Strongylocentrotus purpuratus</i>	Northern and southern California, the USA (subtropical)	Not stated, but likely variable	Settlement pulses were strongly seasonal (spring); however, there was a strong spatiotemporal variability in the number of settlers. Sites in northern, central and southern California were shown to form geographic subunits with respect to coherence in settlement pulses.	Weekly; Feb/Mar 1990–Jul 1993 with exceptions	Scrub brushes with nylon bristles	Ebert et al. (1994)
<i>Strongylocentrotus purpuratus</i>	Southern Oregon, the USA (temperate)	18 m (Port Oxford) & 22 m (Gregory Point)	Settlement occurred, but was generally low from April to August at both locations. Settler densities peaked at Gregory Point in June 1995, while settlement at Port Oxford was highest in late July–early August 1994 and March–April 1995. Settlement pulses were generally associated with warm–water events characterised by a mixed water column and northward wind stress.	Deployments ranging from 9 to 35 days; Feb–Aug in 1994 and 1996	AstroTurf inside PVC pipe	Miller & Emlet (1997)
<i>Strongylocentrotus purpuratus</i>	Southern & northern California, the USA (subtropical)	Shallow subtidal and intertidal rocky habitats	Settlement varied greatly, both inter- and intra-annually, at all three locations over 27 years. Following a seasonal pattern with peak settlement during April–May, settlement fluctuations were highly synchronous among sites within Southern California locations. Large spatiotemporal settlement patterns were related to differential responses to fluctuations in ocean temperature and climate.	Weekly (1990–2003) and fortnightly (2003–2016)	Scrub brushes with nylon bristles	Okamoto et al. (2020)
<i>Strongylocentrotus purpuratus</i> & <i>Mesocentrotus franciscanus</i>	Santa Barbara, the USA (subtropical)	Urchin barren grounds and kelp beds	Newly settled echinoids were found in low numbers from April to July in 1984 and 1985, and in April 1986. In early May 1986, many settlers of both species were present in high numbers on both foliose red algal turf and crustose coralline algae substrata.	Irregular sampling frequency; 1984–1986, mostly during summer	Collection of reef shale pieces	Rowley (1989)

(Continued)

Table 3 (Continued) Summary of studies assessing spatial and temporal settlement patterns in echinoids

Species	Location (climate)	Habitat; depth	Patterns observed	Sampling frequency; dates	Methodology	Reference
<i>Strongylocentrotus purpuratus</i> & <i>Mesocentrotus franciscanus</i>	Monterey Bay, the USA (subtropical)	Kelp forest; 10 m	Two distinct peaks in settlement occurred from December through February and April through July.	Monthly; Jul 1988–Jul 1989	Plastic matrix or articulated coralline algae inside a PVC pipe	Harrold et al. (1991)
<i>Strongylocentrotus purpuratus</i> & <i>Mesocentrotus franciscanus</i>	Northern California, the USA (subtropical)	Rocky habitat; 10–12 m	The total seasonal settlement rate varied substantially among the locations sampled. While very few settlers were recorded at Duxbury Reef, Bodega Head and Salt Point, while settlement was markedly higher at Point Reyes.	Weekly; Apr–early Sep 1993	Scrub brushes with polypropylene bristles	Wing et al. (1995a)
<i>Strongylocentrotus purpuratus</i> & <i>Mesocentrotus franciscanus</i>	Northern California, the USA (subtropical)	Rocky habitat; 5–20 m	Settlement occurred at low levels from late April to late July, and synchronous peaks were reported at both locations in mid-July.	Weekly; Apr–early Sep 1992	Scrub brushes with polypropylene bristles	Wing et al. (1995b)
<i>Strongylocentrotus purpuratus</i> & <i>Mesocentrotus franciscanus</i>	Southern California, the USA (subtropical)	Kelp forest, inshore and offshore habitats; 12–15 m	Settlement was generally low (0–10 settlers per collector) across locations in both years, and there was no evidence of lower settlement rates of either species at sites situated under the kelp canopy as opposed to offshore sites.	Weekly (5–20 days); Mar–May 1991, Jan 1992 and Apr–Jul 1992	Scrub brushes with nylon bristles	Schroeter et al. (1996)
<i>Strongylocentrotus nudus</i>	Hokkaido, Japan (temperate)	Rocky substratum; 1–9 m	Settlement annually occurred at generally low densities between 1980 and 1995, with the exception of a strong settlement pulse recorded in 1984. Relatively high densities of newly settled echinoids were also found in 1990–1992 and 1995. Settler densities varied between the two sampling locations Okushiri Island and Shimamaki.	Annually; Aug or Sep from 1980 to 1995, excluding 1981 and 1983	Underwater visual quadrat survey	Agatsuma et al. (1998)
Echinoid spp. (i.a. <i>Mespilia globulus</i> and <i>Echinometra</i> sp.)	Central Great Barrier Reef, Australia (tropical)	Coral reef; 15 m	Numbers of echinoid settlers were generally high at all sites, although settlement was significantly greater at the front reef sites than on the back reef sites.	Single deployment for 2 months from Nov 1991 to Jan 1992	Plastic bioballs inside net bags	Keesing et al. (1993)

Table 4 Summary of studies assessing spatial and temporal settlement patterns in asteroids

Species	Location (climate)	Habitat; depth	Patterns observed	Sampling frequency; dates	Methodology	Reference
<i>Acanthaster cf. solaris</i>	Suva Barrier Reef, Fiji (tropical)	Coral reef; shallow depth (crest)	A major settlement pulse only occurred in one (1984) of the nine sampling years (1979–1987). The low number of newly settled asteroids recorded in most years is likely the ‘normal’ amount of settlement success, while unusually high settlement of larvae in some years may give rise to population irruptions.	Monthly to annually; 1979–1987	Quadrat searches for newly settled individuals	Zann et al. (1987)
<i>Acanthaster cf. solaris</i>	Central Great Barrier Reef, Australia (tropical)	Coral reef; 15 m	Low numbers of settlers were found in the artificial collectors during the summer sampling period (late November to late February). Settlement was only observed at two front reef sites, while no settlers were recorded at any of the back reef sites.	Single deployment for 2 months from Nov 1991 to Jan 1992	Plastic bioballs inside net bags	Keesing et al. (1993)
<i>Acanthaster cf. solaris</i>	Moore Reef, Australia (tropical)	Coral reef; 2–9 m	Settlement occurred between October 2016 and February 2017. The settlement pulse was stronger between December and March than between October and February.	Oct 2016–Feb 2017, Dec 2016–Mar 2017	Plastic bioballs inside leaf baskets	Uthicke et al. (2019)
<i>Acanthaster cf. solaris</i>	Central Great Barrier Reef, Australia (tropical)	Coral reef; 1–18 m	Densities of settlement-stage individuals were highest at intermediate depths (8–14 m), and increased and decreased with the availability of rubble and coral substrata, respectively. At the reef scale, settler density was greatest in south-western and northern fore reef habitats.	May and Jun 2017	Underwater visual quadrat survey	Wilmes et al. (2020)
<i>Acanthaster cf. solaris</i>	Northern and central Great Barrier Reef, Australia (tropical)	Coral reef; 4–12 m	Settlement varied considerably among sampling periods and peaked between October 2016 and January 2017. Reports substantial latitudinal variation as collectors deployed in the central GBR were > ten times more likely to record settlers than in the northern GBR. No preferential settlement was detected among depths, suggesting these larvae readily settle in shallow reef environments.	Four sampling periods: Oct 2016–Jan 2017; Dec 2016–Mar 2017; Nov 2017–Feb 2018; and Nov 2019–Feb 2020	Plastic bioballs inside leaf baskets	Doll et al. (2021)
<i>Asterias forbesi</i>	Long Island Sound, the USA (temperate)	3–9 m	Settlement mostly occurred between early July and early September for an average period of 52 days, but the timing and length of the settlement period varied between years. Settlement was also highly variable among the three areas and ten nested sites; however, settler densities were remarkably similar among the three depths studied (3, 6 and 9 m) at any given year.	Twice per week; 1937–1961	Shells inside collectors	Loosanoff (1964)
<i>Asterias forbesi</i> & <i>A. vulgaris</i>	Nova Scotia, Canada (temperate)	Kelp bed and urchin barren ground; 5–10 m	Settlement was generally high, but variable among years and occurred from late July to early October. Higher densities of settlers were observed in and above kelp beds than in the urchin barrens.	Fortnightly: Jun–Nov 1992, May–Nov 1993 and Jun–Oct 1994	AstroTurf inside PVC pipe	Balch & Scheibling (2000)

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Table 4 (Continued) Summary of studies assessing spatial and temporal settlement patterns in asteroids

Species	Location (climate)	Habitat; depth	Patterns observed	Sampling frequency; dates	Methodology	Reference
<i>A. forbesi</i> & <i>A. rubens</i>	Bocabec Cove, Canada (temperate)	Rocky subtidal zone	Highly variable settlement among years, intra-annual sampling periods and sites. Settlement peaked from early August to early September 2005. Settler densities were lower in 2004 and peaked later. Highest densities for both years were recorded at the site closest to the larger body of water, Passamaquoddy Bay. If transported to the area by currents, larvae would likely reach this site first and, if competent, settle.	Fortnightly; Jun–Oct 2004, Jun–Oct 2005	AstroTurf inside PVC pipe	Jennings & Hunt (2010)
<i>Choriaster granulatus</i>	Central Great Barrier Reef, Australia (tropical)	Coral reef; 15 m	Low numbers of settlers were recorded at front and back reef sites during the summer sampling period (late November to late February).	Single deployment for 2 months from Nov 1991 to Jan 1993	Plastic bioballs inside net bags	Keesing et al. (1993)
<i>Coscinaasterias muricata</i>	Wellington region, New Zealand (temperate)	Rocky reef; 4–7 m	Highly variable settlement among sampling years and locations. Settlers were highly abundant in 2019 at two locations (Kau Bay & Shelly Bay), and a smaller pulse of settlement occurred in 2017 at the same sites. Overall echinoderm settlement pulses were positively correlated with seawater temperature, chlorophyll and shell cover (exclusively found at these Harbour sites).	Annually; Nov 2016–Apr 2017, Nov 2017–Apr 2018, Dec 2018–Feb 2019	Plastic bioballs inside nylon net	Glockner-Fagetti & Phillips (2020)
<i>Culcita novaeguineae</i>	Central Great Barrier Reef, Australia (tropical)	Coral reef; 15 m	Low numbers of settlers were found in the artificial collectors during the summer sampling period (late November to late February). Settlement was only observed at one back reef site and two front reef sites.	Single deployment for 2 months from Nov 1991 to Jan 1994	Plastic bioballs inside net bags	Keesing et al. (1993)
<i>Asteroid</i> sp.	Northern California, the USA (subtropical)	Rocky habitat; 5–20 m	Settlement occurred at low levels from early April to late July and peaked in mid-July at the Bodega Marine Laboratory location. At Salt Point, a strong, synchronous settlement pulse was recorded in mid-late July, but settlement was absent before and after.	Weekly; Apr–early Sep 1992	Scrub brushes with polypropylene bristles	Wing et al. (1995b)
<i>Asteroid</i> sp. A	Wellington region, New Zealand (temperate)	Rocky reef; 4–7 m	Inter-annual and spatial variation in settlement observed. Settlement occurred in 2018 and 2019 at Princess Bay and Breaker Bay. Overall echinoderm settlement pulses were positively correlated with shell cover, seawater temperature and chlorophyll.	Annually; Nov 2016–Apr 2017, Nov 2017–Apr 2018, Dec 2018–Feb 2020	Plastic bioballs inside nylon net	Glockner-Fagetti & Phillips (2020)
<i>Asteroid</i> sp. B	Wellington region, New Zealand (temperate)	Rocky reef; 4–7 m	Little settlement occurred in 2019 at Princess Bay. Overall echinoderm settlement pulses were positively correlated with shell cover, seawater temperature and chlorophyll.	Annually; Nov 2016–Apr 2017, Nov 2017–Apr 2018, Dec 2018–Feb 2021	Plastic bioballs inside nylon net	Glockner-Fagetti & Phillips (2020)

Table 5 Summary of studies assessing spatial and temporal settlement patterns in ophiuroids

Species	Location (climate)	Habitat; depth	Patterns observed	Sampling frequency; dates	Methodology	Reference
<i>Amphiura chitaei</i>	Øresund, Denmark (temperate)	Muddy sand; 27 m	Settlers were observed in relatively small numbers, and the settlement period was found to start in early November in 1964, which was 3 months later than in <i>Amphiura filiformis</i> .	Fortnightly; Oct 1963–Oct 1966	Mouse-trap sampler	Muus (1981)
<i>Amphiura filiformis</i>	Øresund, Denmark (temperate)	Muddy sand; 27 m	Settlement occurred annually between August and December and peaked during a 2- to 6-week period in September to November.	Fortnightly; Oct 1963–Oct 1965	Mouse-trap sampler	Muus 1981
<i>Amphiura filiformis</i>	Galway Bay, Ireland (temperate)	Silty sand; 20 m	Little settlement over the 8-year period as only approximately 5% of the population were newly settled individuals (<4 mm). Settlement likely peaked in the autumn months from September to November.	3–10 monthly samples; 1974–1976	Van Veen grab and diver-operated suction sampling	O'Connor et al. (1983)
<i>Amphiura filiformis</i>	German Bight & North Sea (temperate)	Muddy sand; 38 and 54 m	Suggests the annual settlement season begins in July to August and the timing of settlement likely progresses from SW to NE during the summer and autumn months.	Every Mar/Apr in 1983, 1984 and 1986 to 1988; also in Jun, Jul/Aug, and Nov in 1983 and 1987, and in Dec 1987	Van Veen grab and Reineck box sampling	Künitzer (1989)
<i>Ophiocten gracilis</i>	Rockall Trough, NE Atlantic (temperate)	Silty sand; 600–1200, 2200 and 2900 m	Highest densities of settlers were recorded during sampling at depths of approximately 2900 m in May and July 1975, June 1978 and May 1980.	Sampling every 2–7 months; May 1975–Sep 1980	Epibenthic sled sampling	Gage & Tyler (1981a)
<i>Ophiocten gracilis</i>	Rockall Trough, NE Atlantic (temperate)	1000 m and 1400 m	Settlement occurred in both traps (1000 m, 1400 m) during mid-May.	May–Jul 1996	Sediment traps	Sumida et al. (2000)
<i>Ophioderma longicaudum</i>	Canary Islands, Spain (subtropical)	Four subtidal habitats: seagrass meadows, urchin barrens, macroalgal beds and sandy patches; 5–10 m	Densities of newly settled ophiuroids differed substantially among the four habitats surveyed, with collectors deployed in macroalgal beds reporting greater numbers than in the other habitats.	Single deployment for 4 weeks from early Aug to early Sep 2008	(A) plastic leaf-like units; (B) cushion-shaped, leaf-like units; and (C) cushion-shaped units	García-Sanz et al. (2012)

(Continued)

Table 5 (Continued) Summary of studies assessing spatial and temporal settlement patterns in ophiuroids

Species	Location (climate)	Habitat; depth	Patterns observed	Sampling frequency; dates	Methodology	Reference
<i>Ophiomereis reticulata</i>	Baleeiro Isthmus, Brazil (subtropical)	Intertidal rock boulder habitat	Analysis of recruitment patterns suggests intense settlement pulses in February and from September to November.	Jan 2001–Dec 2002	-	Yokoyama & Amaral (2011)
<i>Ophiopholis aculeata</i> and <i>Ophiura</i> spp.	Nova Scotia, Canada (temperate)	Kelp bed and urchin barren ground; 5–10 m	Within the annual 2-week settlement period, a major settlement pulse occurred over a 3-day interval, and settlement declined over the following 6 days. This settlement pulse was preceded by rapid temperature and salinity fluctuations and related to a change in current direction.	Three-day intervals during 2-week settlement period in Jul/Aug 1993	AstroTurf inside PVC pipe	Balch et al. (1999)
<i>Ophiopholis aculeata</i> and <i>Ophiura</i> spp.	Nova Scotia, Canada (temperate)	Kelp bed and urchin barren ground; 5–10 m	Settlement was observed from July to early August each year. Spatial differences in settlement between sites were likely related to variable larval supply due to local differences in hydrodynamic conditions. Settlement rates were higher in the barrens than in kelp beds, and substantially more settlers were collected in the high (2.3 m off bottom) than in the low (0.2 m) collectors.	Fortnightly; Jun–Nov 1992, May–Nov 1993 and Jun–Oct 1994	AstroTurf inside PVC pipe	Balch & Scheibling (2000)
<i>Ophiotrix fragilis</i>	Blanes, Spain (temperate)	Subvertical rocky walls & sandy bottom; 8–12 m	Compared the pattern found after settlement had ceased (July 1997 survey) with that found while settlement was still under way (June 1999 survey). Settlement occurred in multiple batches and peaked in June.	July 1997 and June 1999	Grab sampling of paired sponge-paired turf samples	Turon et al. (2000)
<i>Ophiura ljungmani</i>	Rockall Trough, NE Atlantic (temperate)	Silty sand; 2260–2925 m	Settlement occurs annually in summer, but the timing and magnitude of settlement likely varies among years.	Irregular sampling frequency; Jan 1979–Sept 1980	Epibenthic sled sampling	Gage & Tyler (1981b)
Ophiuroid species	Central Great Barrier Reef, Australia (tropical)	Coral reef; 15 m	High numbers of ophiuroid settlers were sampled at both the front reef and back reef locations. While no difference in settlement rates was observed between these two locations, settlement was patchy, with variable rates at the scale of hundreds of metres.	Single deployment for two months from Nov 1991 to Jan 1992	Plastic bioballs inside net bags	Keesing et al. (1993)
Ophiuroid species	Wellington region, New Zealand (temperate)	Rocky reef; 4–7 m	Settlers were recorded continuously from year to year; however, significant spatial variation was recorded. Settlement occurred during all three sampling years at Princess Bay and Beaker Bay, and little settlement occurred in 2017 at Moa Point. These sites had relatively high macroalgal cover.	Annually; Nov 2016–Apr 2017; Nov 2017–Apr 2018; Dec 2018–Feb 2019	Plastic bioballs inside nylon net	Glockner-Fagetti & Phillips (2020)

Table 6 Summary of studies assessing spatial and temporal settlement patterns in holothuroids

Species	Location (climate)	Habitat; depth	Patterns observed	Sampling frequency; dates	Methodology	Reference
<i>Australostichopus mollis</i>	Wellington region, New Zealand (temperate)	Rocky reef; 4–7 m	Settlement occurred only in 2017 and 2019 at Shelly Bay. Overall echinoderm settlement pulses were positively correlated with shell cover, seawater temperature and chlorophyll.	Annually; Nov 2016–Apr 2017; Nov 2017–Apr 2018; Dec 2018–Feb 2019	Plastic bioballs inside nylon net	Glockner-Fagetti & Phillips (2020)
<i>Cucumaria frondosa</i>	St. Lawrence Estuary, Canada (temperate)	Rocky subtidal zone; 0–60 m	Newly settled individuals were predominantly found at shallow depth between 0 and 20 m, rare between 20 and 40 m and virtually absent below 40 m. The highest densities of settlers were recorded in areas with high cover of gravel, small rocks and boulders, and also high light availability.	Seasonally; at the beginning of each season from spring 1992 to winter 1994	Belt transect surveys	Hamel & Mercier (1996)
<i>Leptosynapta clarki</i>	Vancouver Island, Canada (temperate)	Mid-intertidal mudflat	Unimodal settlement likely occurred in both years around February to March prior to annual recruitment pulses in April to May.	Bi-monthly; May 1990–Aug 1991	Sediment coring	Sewell (1994)
<i>Pentamera chierchia</i> & <i>Neothyone gibber</i>	Marietas Islands, Mexico (tropical)	Coral reef with sandy and rocky bottom areas	Recruitment density presented seasonal changes, with peaks for both species in May to June, and low recruitment for the rest of the year. This peak is suggested to be due to a settlement event following the March–April spawning time. Thus, a pulse in settlement likely occurred in April or May.	Bi-monthly; Mar 2011–Feb 2012	Coral skeletal structures as settlement collectors	Sotelo-Casas et al. (2016)
Holothuroid spp. (mostly <i>Psolus fabricii</i> , and few <i>Cucumaria frondosa</i>)	Bocabec Cove, Canada (temperate)	Rocky subtidal zone	Settler densities varied substantially between and within years; however, no spatial variation in settlement was reported. Only one settler was found during 2004, while high settlement pulses were detected in July 2005 at multiple sites.	Fortnightly; Jun–Oct 2004; Jun–Oct 2005	AstroTurf inside PVC pipe	Jennings & Hunt (2010)

(e.g. Zann et al. 1987). However, as demonstrated for the asteroids *Asterias forbesi* (Loosanoff 1964) and *Acanthaster cf. solaris* (Keesing & Halford 1992), and the echinoid *Strongylocentrotus purpuratus* (Rowley 1989), high larval settlement rates do not always give rise to high rates of recruitment to juvenile and adult populations. Conventional field-based studies usually only detect newly settled individuals that have had time to grow (e.g. Wilmes et al. 2020), such that it is very likely that differential post-settlement survival will have already modified patterns of abundance established at settlement. Visual underwater searches within quadrats or transect belts have reported densities of settlers soon after predicted settlement for echinoids (Hunte & Younglao 1988, Agatsuma et al. 1998), asteroids (Wilmes et al. 2020) and holothuroids (Hamel & Mercier 1996). Densities of recently settled ophiuroids have mostly been studied using various grab samplers, including mouse-trap samplers, Van Veen grab samplers, sled samplers and sediment traps (Gage & Tyler 1981a,b, Muus 1981, O'Connor et al. 1983, Künitzer 1989, Sumida et al. 2000). These techniques usually limit ophiuroid studies to few and short sampling intervals (Table 5); however, the logistical difficulties of sampling such cryptic settlers, particularly in deep-sea habitats, do not allow extensive sampling designs as seen in some shallow-water echinoderm taxa (e.g. Ebert et al. 1994). Conventional underwater surveys, inferences based on adult densities or back-calculations based on size distributions (e.g. Yokoyama & Amaral 2011) almost invariably lack data on early post-settlement processes, including mortality rates, to effectively represent settlement patterns (Keesing et al. 2018). Mortality may be very high during this period due to individuals adapting to the new benthic habitat and exposure to a new suite of predators (Wilmes et al. 2018), necessitating novel approaches of sampling individuals during or soon after settlement.

To address the inherent limitations in recording settlement in natural substrates and habitats, various different artificial settlement collectors have been employed (Loosanoff 1964, Bak 1985, Harrold et al. 1991, Keesing et al. 1993, Ebert et al. 1994, Lamare & Barker 2001, Uthicke et al. 2019). It is not clear how rates of settlement and early post-settlement survival differ between these artificial collectors and natural substrata, such that the collectors only allow relative comparisons of settlement potential, as opposed to absolute rates of larval settlement (Keesing et al. 1993). Early deployment, prior to anticipated settlement, to allow for extensive pre-conditioning and colonisation of the collectors could mitigate, but not resolve this limitation. If absolute rates of settlement had to be obtained (e.g. for stock-recruitment modelling), experimental assays comparing settlement rates and early post-settlement mortality on natural and conditioned artificial substrata could provide an indication of differential inductive capacity and survival. Potential differences could be then applied when calculating settlement rates for a reef area based on settler densities found in artificial collectors. In any case, these artificial collectors facilitate separation of settlement from post-settlement processes to produce a more accurate census of settlers and have thus been widely used in recent decades. More than two-thirds of the 53 studies on echinoderm settlement patterns summarised here used some form of artificial settlement collector (Figure 4), and some of these studies compared the relative efficiency of multiple collector designs for quantitative assessments of echinoderm settlement rates (Lamare & Barker 2001, Hereu et al. 2004, García-Sanz et al. 2012, Balsalobre et al. 2016). In general, these artificial samplers are designed to maximise microhabitat complexity and surface area, which is favourable for settlement and metamorphosis (Hunte & Younglao 1988, Harrold et al. 1991, Keesing et al. 1993). Moreover, these methods minimise disturbance to the benthos and can be easily deployed and retrieved for variable sampling durations and intervals.

Artificial turf panels, scrubbing brushes and some other similar collector designs are commonly used to assess spatiotemporal settlement patterns in echinoids (Figure 4), but have also been shown to facilitate settlement of ophiuroids, asteroids and holothuroids in the field (Wing et al. 1995b, Balch et al. 1999, Balch & Scheibling 2000, Jennings & Hunt 2010). Both types of sampling devices are usually suspended vertically in the water column, either from overhanging ledges from shore, or anchored to the substratum. Harrold et al. (1991) examined *Strongylocentrotus purpuratus*

settlement using pieces of PVC pipe, which were filled with either high surface area plastic matrix or articulated coralline algae and suspended 1 m above the substratum. Higher densities of settlers were recorded in the designs using the plastic matrix, although this may have been due to a higher number of predators in the coralline algal collectors (Harrold et al. 1991). This design was later modified by Miller & Emllet (1997) and Balch et al. (1998) who lined PVC pipes with plastic turf, which is an effective settlement surface for echinoids (Harris et al. 1994) and has frequently been used in subsequent studies (Balch & Scheibling 2000, Lambert & Harris 2000, Jennings & Hunt 2010). Balch & Scheibling (2000) demonstrated the utility of suspending collectors in the water column for mitigating the potential effects of early post-settlement mortality due to predation, as substantially more ophiuroid settlers were collected in the high (2.3 m off bottom) than in the low (0.2 m) collectors.

Scrubbing brushes with nylon bristles were first used by Ebert et al. (1994) to document settlement rates of the echinoids *Mesocentrotus franciscanus* and *Strongylocentrotus purpuratus*. Due to their ease of use and cost-effectiveness, scrubbing brushes are still widely used (e.g. Schroeter et al. 1996, Okamoto et al. 2020). Studying *Evechinus chloroticus* settlement in New Zealand, Lamare & Barker (2001) compared scrubbing brush samplers (Ebert et al. 1994), AstroTurf panels (Ebert et al. 1991) and PVC pipes filled with plastic matrix (Harrold et al. 1991) and found the unstandardised mean number of settlers recovered from the PVC pipe design to be three- to fivefold higher than from the other two sampler designs. Conversely, wooden scrubbing brushes with vegetal bristles recorded considerably higher numbers of settlers than oyster shells, artificial grass and plastic matrix in trials measuring *Paracentrotus lividus* settlement in the Western Mediterranean Sea (Hereu et al. 2004). These comparative assessments reveal that it is probably not viable to compare settlement rates measured using contrasting methods, although most methods in and of themselves will provide insights into settlement patterns.

The settlement collectors designed by Keesing et al. (1993) consisted of a net bag containing 100 plastic aquarium filter bioballs, which provide an extremely high surface area, and successfully sampled settlers of numerous species of asteroids, ophiuroids, crinoids and echinoids on Australia's Great Barrier Reef. Laboratory trials demonstrated that competent larvae of crown-of-thorns starfish (*Acanthaster cf. solaris*) readily settle on plastic surfaces, which had been pre-conditioned in seawater aquaria (Keesing et al. 1993). Aquarium filter bioballs have since been incorporated in various modified versions of these collectors to efficiently sample settlement in a diverse range of habitats and different echinoderm species (Hernández et al. 2006, 2010, Clemente et al. 2009, Uthicke et al. 2019, Glockner-Fagetti & Phillips 2020, Doll et al. 2021). The suitability of this method to sample settlement rates in a wide range of echinoderms was corroborated by quantitative comparisons of multiple collector designs (Balsalobre et al. 2016); nylon nets containing plastic bioballs showed higher reproducibility and efficiency in sampling settlement than vertically oriented scrubbing brushes with vegetal bristles, or horizontal triangular mats of coconut fibre. Other artificial settlement collectors shown to effectively sample echinoid and ophiuroid species include settlement plates consisting of polystyrene egg crates and plexiglass (Bak 1985, Miller et al. 2009, Vermeij et al. 2010, Roger & Lorenzen 2016), and various designs of leaf-like units consisting of plastic mesh frames and plastic raffia (García-Sanz et al. 2012, 2014a).

The biggest constraint to using artificial settlement collector methods is the post-collection process time required to remove, sort and identify newly settled echinoderms, which are often microscopic (Keesing et al. 1993). Moreover, reliable visual identification of newly settled individuals may not be possible, especially if large numbers of sympatric species exist within sampling regions (Keesing et al. 1993). Innovative genetic analyses (e.g. eDNA) have emerged as a promising tool to address these constraints and further the utility of artificial settlement collectors to advance the understanding of settlement patterns (Uthicke et al. 2019, Doll et al. 2021). Uthicke et al. (2019) successfully detected newly settled *Acanthaster cf. solaris* in settlement collectors using taxon-specific mtDNA primers and standard polymerase chain reaction (PCR) (Uthicke et al. 2019). Further tests

by Doll et al. (2021) validated the utility of genetic analyses using digital droplet PCR in assessing spatiotemporal settlement patterns. If developed as an accurate and quantitative tool, this method would be of particular utility for large-scale, high replicate studies of settlement for ecologically important taxa, and echinoderm groups for which reliable visual identification is not possible.

Although artificial settlement collectors cannot be regarded as providing absolute numbers of echinoderm settlers, they certainly provide comparable estimates of spatial and temporal variation in settlement and can complement *in situ* sampling of older juveniles in natural habitats. Simultaneous sampling using both these approaches will allow for improved discrimination between settlement and post-settlement processes (Harrold et al. 1991). Overall, artificial settlement collectors provide a relatively non-destructive sampling method and standardised index to study spatial and temporal settlement patterns for most echinoderm groups. Genetic methods are also likely to reduce processing time and greatly enhance capacity to assess spatiotemporal variability in settlement.

Spatial and temporal patterns of settlement

Echinoidea

Marked seasonality in settlement has been documented in the vast majority of echinoid taxa, and this pattern appears to be consistent among different habitat types and climate zones (Table 3). Species of the genera *Strongylocentrotus* and *Mesocentrotus*, commonly studied along the California coast (Ebert et al. 1994, Wing et al. 1995b, Miller & Emler 1997, Okamoto et al. 2020) and in the western Atlantic (Balch & Scheibling 2000, Lambert & Harris 2000, Jennings & Hunt 2010), predominantly settle between April and July each year. Along the California coast, unimodal settlement peaks or primary settlement pulses occurred in June (Miller & Emler 1997, Okamoto et al. 2020) and July (Wing et al. 1995b). This timing coincides with warmer (or increasing) water temperatures, suggesting that temperature-induced spawning, as observed in other echinoderms (e.g. Caballes et al. 2021), may be governing this pattern. In contrast, Harrold et al. (1991) reported two distinct peaks in the settlement of *Mesocentrotus franciscanus* and *Strongylocentrotus purpuratus* in Monterey Bay, occurring from April through July and December through February, respectively. Ebert et al. (1994) recorded multiple annual settlement pulses, however, all between February and July each year. As part of a 27-year study, Okamoto et al. (2020) demonstrated annual settlement peaks during April and May and strong seasonal settlement fluctuations, which were highly synchronous among sites within Southern California locations. Here, temporal patterns of larval settlement were linked to fluctuations in ocean temperature and climate, which may impact pre-settlement processes and larval supply in *S. purpuratus* (Okamoto et al. 2020). Strong intra-annual variability in settlement rates was further reported for *Evechinus chloroticus* in New Zealand (Lamare & Barker 2001, Walker 2007, Glockner-Fagetti & Phillips 2020). Likewise, major settlement peaks of the echinoid *Paracentrotus lividus* only occurred between February and April on the Canary Islands (García-Sanz et al. 2014b) and between April and June in the Western Mediterranean Sea (Hereu et al. 2004, Tomas et al. 2004). On tropical and subtropical reefs, the echinoid *Diadema antillarum* settles continuously, but in low numbers throughout the year (Bak 1985, Miller et al. 2009, Williams et al. 2010), with substantial settlement pulses detected in the spring and autumn months in Curaçao (Bak 1985, Vermeij et al. 2010), and in July (Williams et al. 2010) or August (Millet et al. 2009) in Puerto Rico. Settlement of *D. africanum* follows a clear unimodal pattern, with a main settlement peak between August and October (Hernández et al. 2006, 2010, García-Sanz et al. 2014), which is probably linked to highly seasonal spawning events in the months prior (Hernández et al. 2006). This strong seasonal settlement pattern is likely directly or indirectly driven by temperature; however, settlement rates may also be negatively affected by reduced food availability in the months prior to settlement (Hernández et al. 2010).

While the timing of annual peaks in the settlement of most echinoids is relatively consistent among years, inter-annual variability in the magnitude of these pulses is generally high (Table 3). Settlement of *Strongylocentrotus nudus* occurred annually at relatively low densities off the north-west coast of Japan, with the exception of a strong settlement pulse in 1984 and some smaller pulses in 1990–1992 and 1995 (Agatsuma et al. 1998). Highly variable settlement among years was also documented for *Mesocentrotus franciscanus* and *Strongylocentrotus purpuratus* off the California coast (Miller & Emler 1997, Okamoto et al. 2020), and *S. droebachiensis* in Nova Scotia (Balch & Scheibling 2000) and Bocabec Cove, Canada (Jennings & Hunt 2010). Similarly, Tomas et al. (2004) and Hereu et al. (2004) reported substantial inter-annual differences in settlement of *Paracentrotus lividus* in the Mediterranean Sea by one and more than two orders of magnitude, respectively. Conversely, settlement rates of *Diadema antillarum* were relatively similar among years in the southern Caribbean Sea, although rates were only monitored over three consecutive years (Bak 1985). High inter-annual variability in *D. africanum* settlement at Canary Islands locations between 2002 and 2008 was likely driven by temperature or food availability during the planktonic larval phase (Hernández et al. 2010). Likewise, Glockner-Fagetti & Phillips (2020) suggested that settlement pulses, which varied considerably among years, were correlated with seawater temperature and chlorophyll concentration. These field studies did not explicitly demonstrate the causative nature of these links; however, the potential effects of starvation (Byrne et al. 2008) and temperature (McEdward 1984, Privitera et al. 2011) on the condition of echinoderm larvae prior and during settlement indicate that these processes may, in fact, be driving temporal settlement patterns.

A range of abiotic factors, including hydrodynamic forces, appear to be driving spatial differences in settlement rates of echinoids, particularly at large scales. Jennings & Hunt (2010) described highly variable settlement of *Strongylocentrotus droebachiensis* among sampling locations. As highest settler densities occurred at the site closest to the larger body of water, larvae transported to the area by currents would reach this site first and settle if competent and stimulated by an inductive cue (Jennings & Hunt 2010). The geographical position in relation to hydrodynamic processes may be an important factor in explaining larger-scale spatial variation in the settlement of other *Strongylocentrotus* species (Wing et al. 1995a, Agatsuma et al. 1998), and echinoids more broadly (Lamare & Barker 2001, Balsalobre et al. 2016). For example, the settlement of *S. droebachiensis* in the Gulf of Maine was one and three orders of magnitude higher than on Nova Scotia's Atlantic Coast and the Bay of Fundy, respectively, indicating substantial differences in larval supply to these locations (Balch et al. 1998). Synchrony in settlement pulses of *S. purpuratus* among geographical subunits off the California coast may be governed by physical processes affecting larval supply at regional scales (Ebert et al. 1994, Okamoto et al. 2020), although *Mesocentrotus franciscanus* did not form such geographic subunits with respect to coherence in settlement pulses (Ebert et al. 1994). At a smaller spatial scale, Clemente et al. (2009) found similar numbers of *Diadema africanum* settlers among sampling locations and sites in the Canary Islands and concluded that larval supply is unlikely to be limiting *D. africanum* settlement at any of the sampled locations. Settler densities of echinoid species, including *Mespilia globulus* and *Echinometra* sp., were generally high across ten sites at Davies Reef on Australia's Great Barrier Reef, although settlement was considerably greater at the front reef sites than on the back reef sites (Keesing et al. 1993). In contrast, settlement rates of *Diadema antillarum* in the southern Caribbean Sea were higher in sheltered lagoons and back reefs than in fore reef habitats (Rogers & Lorenzen 2016). Comparing settlement rates of *Evechinus chloroticus* in the Hauraki Gulf, New Zealand, Walker (2007) found no settlers at a sheltered, high-sediment location, while settler densities were high, although spatiotemporally variable, at a wave-exposed, low-sediment location.

Larval supply and the exposure to physical factors thus appear to also play a role in determining settlement patterns at smaller spatial scales. However, with decreasing spatial scale, taxon-specific chemical cues have been shown to also commonly play an important role in the processes surrounding larval settlement and thus relative rates of settlement at varying sites, habitats and depths.

Hereu et al. (2004) found settlement rates of *Paracentrotus lividus* to relate to wave exposure and currents, but not substratum type or adult densities, suggesting settlement patterns were not driven by chemical stimuli. Conversely, settlement of *P. lividus* was found to be generally higher on vertical rock wall habitats than in seagrass meadows at the same location in the Western Mediterranean Sea (Tomas 2004). García-Sanz et al. (2014) reported the same species to preferentially settle on soft substrata including seagrass, as opposed to hard substrata such as barrens and macroalgal beds, in the Canary Islands. Competent *P. lividus* larvae readily settle in response to chemical cues associated with various substrata (Table 1), including seagrass, brown macroalgae and coralline red algae (Privitera et al. 2011). Thus, the presence of chemical stimuli associated with inductive substrata may be driving these contrasting patterns at different locations.

Settler densities of *Strongylocentrotus droebachiensis* were higher in barren grounds than in adjacent seagrass beds (Balch et al. 1998). Larvae of this species respond to numerous types of coralline algae and red, brown and green fleshy algal species (Rowley 1989, Pearce & Scheibling 1990b, 1991). The main food source of *Strongylocentrotus* spp. is brown macroalgae, with occasional omnivory (Tegner 2001, Scheibling & Hatcher 2007). Competent *S. droebachiensis* larvae are likely induced to settle by a chemical cue associated with their preferred prey or conspecifics present in the urchin barrens, but not the adjacent seagrass beds. Similarly, the relatively high densities of *Diadema africanum* in urchin barren habitats, compared to macroalgal beds (Hernández et al. 2010, García-Sanz et al. 2014) and/or seagrass meadows (García-Sanz et al. 2014a), may be driven by gregarious settlement cues, which have been demonstrated in other echinoid species (Highsmith 1982, Burke 1984, Highsmith & Emler 1986, Pearce & Scheibling 1990a, Dworjanyn & Pirozzi 2008, Mos et al. 2011, Ling et al. 2019). Differential settlement of echinoids along depth gradients has only been assessed in two studies. Larvae of both *Paracentrotus lividus* and *Strongylocentrotus droebachiensis* preferentially settled at shallow depths, with decreased settlement rates reported below 10m (Harris et al. 1994, Hereu et al. 2004). In the case of *P. lividus*, this pattern is likely governed by physical processes or cues affecting larval movement or behaviour, as the results of this study suggest that the rocky substratum, although colonised by a rich algal assemblage, is not a cue for its settlement (Hereu et al. 2004).

Asteroidea

Available evidence suggests the settlement of asteroids is also highly variable within and among years (Table 4), although much of the research to date has focused on two genera, the corallivorous crown-of-thorns starfish (*Acanthaster* spp.) on coral reefs (Zann et al. 1987, Keesing et al. 1993, Uthicke et al. 2019, Wilmes et al. 2020, Doll et al. 2021), and asteroids of the genus *Asterias* in North America (Loosanoff 1964, Balch & Scheibling 2000, Jennings & Hunt 2010). Loosanoff (1964) monitored settlement rates of the temperate asteroid *Asterias forbesi* using shells inside collectors at Long Island Sound for bi-weekly intervals from 1937 to 1961. Settlement of *A. forbesi* predominantly occurred between early July and early September for a mean duration of 7 weeks; however, both the annual timing and the duration of this settlement period varied among years (Loosanoff 1964). This high inter-annual variability of settlement in this asteroid was further confirmed by Jennings & Hunt (2010) off Canada's Atlantic Coast. Here, settlement of *A. forbesi* and *A. rubens* peaked around the same time in 2005, from early August to early September, but settler densities were considerably lower in the last year (Jennings & Hunt 2010). Likewise, Balch & Scheibling (2000) reported generally high, but variable settlement among years for *A. forbesi* and *A. vulgaris* in the same region. Temporal trends, such as the highly variable settlement among sampling years of *Coscinasterias muricata* in New Zealand, are likely governed by the timing of pre-settlement processes and variable larval supply, as settlement pulses of *C. muricata* were positively correlated with larval food availability and seawater temperature (Glockner-Fagetti & Phillips 2020). Similar biotic and abiotic factors may be driving inter-annual differences in settlement observed in other

asteroid species, such as *Stichaster australis* in New Zealand (Barker 1979). In Fiji, Zann et al. (1987) observed a major settlement pulse of *Acanthaster cf. solaris* in only one of the nine sampling years from 1979 to 1987. The low number of settlers recorded in most years was suggested to represent 'normal' settlement events, while spikes in the abundance of settlers in some years may give rise irruptive population growth (Zann et al. 1987).

Temporal settlement variability within (Uthicke et al. 2019) and among years (Doll et al. 2021) has only recently been explicitly demonstrated for crown-of-thorns starfish. However, the marked temporal patterns and propensity to undergo major population irruptions displayed by *Acanthaster cf. solaris* (Pratchett et al. 2014) are most likely linked to differential rates of larval supply (Birkeland 1982, Brodie et al. 2005), settlement and subsequent early post-settlement processes. It is unclear whether strong pulses and inter-annual differences in the settlement of both *A. cf. solaris* and *Asterias* spp. are driven by adult population density fluctuations of these species (Uthicke et al. 2009), or whether it is, in fact, settlement patterns that drive these adult population fluctuations in the first place.

Settlement patterns of both *Acanthaster cf. solaris* and *Asterias* spp. are also highly variable among regions and locations throughout their geographical ranges (Loosanoff 1964, Jennings & Hunt 2010, Doll et al. 2021). In the case of *Acanthaster cf. solaris*, spatial patterns of larval settlement on the Great Barrier Reef likely depend on spatiotemporal availability of larvae, driven by the latitudinal progression of their population irruptions, with regional estimates of settlement coinciding with densities of adult asteroids (Doll et al. 2021). Settlement of asteroid species is also highly variable at smaller spatial scales. Settlement of *Coscinasterias muricata* was high at two sites inside the Wellington Harbour, New Zealand, but completely absent at the three sites on the southern coast and the mouth of the harbour (Glockner-Fagetti & Phillips 2020). At this localised scale, such contrast in settlement success may be driven by substratum-related cues, as shell cover was exclusively found in the harbour and correlated with echinoderm settlement pulses overall (Glockner-Fagetti & Phillips 2020).

Similarly, physical or chemical cues acting at the site or habitat scale may also play a role in the smaller-scale settlement patterns displayed by these asteroids (Keesing et al. 1993, Balch & Scheibling 2000, Wilmes et al. 2020). For example, densities of juvenile *Acanthaster cf. solaris* (approx. 6 months post-settlement) were positively related to the cover of rubble, and more commonly observed in fore reef as opposed to back reef habitats (Keesing et al. 1993, Wilmes et al. 2020). Settlement of competent *A. cf. solaris* larvae in response to cues from some crustose coralline algae species (preferred settlement substratum and juvenile prey; Wilmes et al. 2020) and associated biofilms are well established (Johnson et al. 1991, Johnson & Sutton 1994). Thus, the availability of rubble beds encrusted with certain species of crustose coralline algae appears to govern the settlement patterns of this species within reefs. The high occurrence of coral rubble supporting epilithic crustose coralline algae at the base of reef slopes in deep water has led to the hypothesis that *A. cf. solaris* larvae predominantly settle on these deep-water habitats (Johnson et al. 1991). However, both their preferred substratum and settlers are also commonly found in shallow water environments in other studies (Wilmes et al. 2020, Doll et al. 2021). Doll et al. (2021) found no difference in settlement among three depth ranges sampled between 4 and 12 m, and records of newly settled *A. cf. solaris* across a wide range of depths (1–18 m) (Wilmes et al. 2020) support the conclusion that *A. cf. solaris* readily settle in shallow water environments. Similarly, settlement rates of *Asterias forbesi* were remarkably similar among three shallow water depths (3–9 m) assessed at any given year (Loosanoff 1964). These studies suggest that it is the presence of particular reef substrata and associated chemical cues, rather than depth, that is driving reef-scale settlement patterns of *Acanthaster cf. solaris* and other asteroids showing strong substratum selectivity.

Ophiuroidea

Compared to other echinoderm classes, the magnitude and timing of ophiuroid settlement appears to be relatively consistent (Table 5). Studies on *Ophiocten gracilis* (Gage & Tyler 1981a, Sumida et al. 2000) and *Ophiura ljunghmani* (Gage & Tyler 1981b) indicate that settlement in these deep-sea ophiuroids occurs annually at the Rockall Trough in the East Atlantic. Highest densities are generally recorded during early summer in May and June, across a wide range of deep-sea sampling depths (Gage & Tyler 1981a, Sumida et al. 2000). Spatial settlement patterns remain largely unexplored; however, a range of physical processes affecting larval supply and advection in deep-sea environments may generally be driving recruitment in these species (Ebert 1983). Ophiuroid larvae can randomly metamorphose in the plankton and then settle indiscriminately (Hendler 1991, McEdward & Miner 2001, Morgan & Jangoux 2005, Selvakumaraswamy & Byrne 2006), which suggests that chemical cues associated with the substratum are unlikely to play an important role, especially given that such deep-sea habitats are characterised by relatively uniform soft substrata (Gage & Tyler 1981a,b).

Consistent annual settlement seasons have also been observed in ophiuroid species at relatively shallow depths in the North Sea and North-East Atlantic Ocean (Muus 1981, O'Connor et al. 1983, Künitzer 1989). Settlement of *Amphiura filiformis* in Øresund, Denmark, occurred annually between August and December and peaked during a short 2- to 6-week window in September to November (Muus 1981). The seasonal settlement pattern displayed by *A. filiformis* was consistent among temperate locations, as settlement in the North Sea, German Bight and off the Irish coast occurred and peaked during the same months (O'Connor et al. 1983, Künitzer 1989). Similarly, larval settlement of *Ophiopholis aculeata* and *Ophiura* spp. was observed in Nova Scotia, Canada, from July to early August each year (Balch & Scheibling 2000). Here, spatial differences in settler densities between sites appear to be driven by variable larval supply due to differences in hydrodynamic conditions, although settlement rates were also higher in urchin barren grounds than in seagrass beds (Balch & Scheibling 2000). Importantly, spatiotemporal settlement patterns and recruitment may also be influenced by cloning of ophiuroid larvae, if environmental conditions support planktonic existence and dispersal (Balsler 1998, Hart et al. 2021). Settlement of *Ophiothrix fragilis* in the Western Mediterranean Sea took place in several patches and peaked in June (Turon et al. 2000). This ophiuroid species is thought to settle gregariously at times (Warner 1971, Morgan & Jangoux 2004, Morgan & Jangoux 2005), which may enhance the chance of settlement by competent larvae in suitable habitats; however, this link has not been demonstrated in field-based studies.

Holothuroidea

While there has been extensive research on settlement induction (and cues) for sea cucumbers (discussed above), as necessary for aquaculture, there have been few field-based studies that examine settlement patterns or early life-history processes (Table 6). Settlement of *Australostichopus mollis* was only detected at one of five sites in the Wellington region in New Zealand during two sampling years (Glockner-Fagetti & Phillips 2020). Settler densities of holothuroids in Bocabec Cove, Canada, including *Psolus fabricii* and *Cucumaria frondosa*, varied considerably between and within sampling years (Jennings & Hunt 2010). However, settlement patterns did not vary spatially, as high pulses occurred in July 2005 at multiple sites, likely driven by currents differentially affecting larval supply at different points in time (Jennings & Hunt 2010). Newly settled *Cucumaria frondosa* were predominantly found at shallow depths (0–20 m) along a rocky subtidal depth gradient, while settlers were rare and absent in intermediate (20–40 m) and deeper waters (40–60 m), respectively (Hamel & Mercier 1996). The highest number of newly settled individuals was recorded in areas characterised by high cover of gravel, small rocks and boulders, and also high light availability (Hamel & Mercier 1996). In complimentary experimental studies, Hamel & Mercier (1996)

demonstrated strong selectivity for the undersurfaces of rocks and rubble, which may be linked to the high light sensitivity displayed by *C. frondosa* during the settlement phase. Largely photopositive during their substratum search and selection, competent larvae likely react to not only physical cues associated with the substratum, but also light intensity. In laboratory studies, other holothuroid species have also been induced to metamorphose in response to cues associated with seagrass (Mercier et al. 2000, Agudo 2007), brown algae (Agudo 2007), periphytic diatoms associated with biofilms (Ito & Kitamura 1997, Agudo 2007) and conspecifics (Young & Chia 1982); however, the relevance of these results has yet to be tested in their natural environments.

Crinoidea

In contrast to the other echinoderm classes, many groups of crinoid species do not have complex planktotrophic larvae, with lecithotrophic larval types in both pelagic and benthic developmental habitats being more common (Lahaye & Jangoux 1985, McEdward & Miner 2001). Keesing (1993) recorded low numbers of crinoid settlers at Davies Reef on Australia's Great Barrier Reef between November 1991 and February 1992. A dozen crinoid larvae settled at the front reef sites, while only three settlers were found at the back reef sites (Keesing et al. 1993). *Antedon bifida* doliolaria appear to settle selectively and gregariously in aquaria and the field, with larvae most commonly observed near or within adult colonies (Lahaye & Jangoux 1985). Larvae of the planktotrophic crinoid *Florometra serratissima* and the external brooder *Dorometra sesokonis* have also previously been shown to metamorphose in response to conspecific cues (Mladenov & Chia 1983, Obuchi et al. 2010). While there have been no observations of gregarious settlement by these two species in the field, the strong gregarious settlement responses of *Florometra serratissima* in culture suggest that gregarious settlement may play an important role in the formation and maintenance of adult aggregations of *F. serratissima* and many other crinoid species with a planktonic larval stage (Mladenov & Chia 1983).

Future directions in research

There is a suite of environmental stimuli that induce settlement of echinoderm larvae, although the specificity and relative importance of these cues vary greatly among species and classes. Environmental cues are thought to become progressively more important at smaller spatial scales and play a critical role in settlement processes once a planktonic larva has attained metamorphic competence. Physical factors have been demonstrated to induce, inhibit or affect the processes occurring during this phase; however, chemical cues in particular have received considerable attention in echinoderm studies. Despite decades of extensive research effort, specific chemical compounds from environmental inducers of echinoderm settlement have not been explicitly identified, with a few exceptions (e.g. four polyunsaturated fatty acids in Kitamura et al. 1993, 1994; histamine in Swanson et al. 2004). In contrast to some other marine invertebrate taxa (reviewed by Hadfield & Paul 2001), there have only been very few attempts to fully or partially characterise the various chemical cues proven to induce echinoderm settlement. As echinoderm larvae have the ability to settle in response to low molecular-weight, water-soluble chemical cues, these cues need to not only be fully characterised, but also quantified (i.e. relevant concentrations) in the habitat of the species. The challenges in carrying out such purifications and characterisations are large, and often complicated by the polarity of molecules and low concentrations of compounds (Hadfield & Paul 2001), but can be overcome using new methodologies. By isolating the chemical cue produced by an alga from the polar extract by cation-exchange chromatography, Swanson et al. (2004) presented evidence that histamine, an invertebrate neurotransmitter, is an important natural inducer of echinoid settlement, correcting the characterisation in a previous study (Williamson et al. 2000). Larvae perceived low concentrations of histamine and responded rapidly to the inducer, and the characterisation was further corroborated by analyses of histamine concentrations in various algae and in the seawater surrounding the most

inductive alga (Swanson et al. 2004, 2006, 2012). Similarly, the physiology and settlement ecology of many other echinoderms could be linked, if chemical cues are fully characterised.

The roles played by biofilms as cues in echinoderm settlement are much more widespread and complex than formerly thought. When tested in isolation from the substratum, many studies have identified biofilms, and associated bacteria or diatoms, as the 'true' inducer of settlement in echinoderms (e.g. Huggett et al. 2006). Previous settlement assays that did not differentiate biofilms from the underlying substrata may thus be of limited use in drawing conclusions about echinoderm settlement behaviour in the field. At the same time, the specific chemical components of biofilms, which serve as cues for settlement in larvae, are largely unknown. Portions of complex protein-lipopolysaccharides, which make up much of the extracellular polymeric substances secreted by microorganisms, have been suggested as a cue (Hadfield 2011); however, such evidence is generally weak, especially for water-soluble cues. Many past studies on the effects of biofilms tested single-taxon cultures of bacteria or other microorganisms in their assays, which does not allow generalisations about larval responses under natural conditions, but nevertheless progresses the identification of specific chemical components that may be important inducers or inhibitors of echinoderm settlement. The development of new *omic* techniques certainly presents an opportunity to characterise microbes in biofilms and generally enhance our understanding of specific receptors and genes responsible for settlement processes in echinoderms (reviewed by Dobretsov & Rittschof 2020). To gain a greater understanding of the ecological and developmental processes surrounding settlement, it is critical not only to test how widespread and relatively important biofilm-induced and bacteria-mediated settlement is among echinoderm taxa, but also to identify the specific chemical components of biofilms which serve as cues. More generally, research on chemosensory-mediated settlement behaviour could also facilitate our ability to address ecological issues, such as population irruptions of the corallivorous crown-of-thorns starfish (Pratchett et al. 2014). While there is likely a multitude of semiochemicals detectable by echinoderm larvae, the characterisation of the few that regulate their behaviour, such as the movement towards or away from the source, could inform the management of such a complex issue (Hall et al. 2017, Motti et al. 2018). Different echinoderm species are likely to respond to different suites of distinct chemical or biochemical cues, but early work has demonstrated that there are many common features to inductive and inhibitory factors.

Further descriptive studies of larval responses to single physical or chemical cues in nature are unlikely to improve our general understanding of the mechanisms driving these processes. There have been numerous studies on the role of physical factors in settlement behaviour (e.g. turbulence), and even more on the induction of settlement by chemical cues, commonly associated with substrata or conspecifics. A considerable shortcoming of these studies has been the highly unnatural conditions in which these effects were tested, as echinoderm larvae do not encounter these environmental cues in isolation in the field. The relevance and potential applications of these cues in the natural environment thus remain largely unknown. Specifically, most studies tested these isolated cues in small containers and in the absence of flow. Larval settlement in echinoids is enhanced by turbulence through a competence shift and short-term behavioural responses facilitating substratum contact (Gaylord et al. 2013, Ferner et al. 2019). Hydrodynamic processes may play an underappreciated role in the induction of echinoderm settlement at the habitat scale and should thus be integrated into settlement assays. Chemical cues associated with substrata and conspecifics could be tested under more realistic flow regimes, and additionally, other physical factors such as light intensity could be considered. Concomitant efforts towards advancing our ability to track larval movements in the field would complement this research. Testing a suite of environmental cues is a non-trivial challenge, but natural conditions must be replicated as closely as possible when studying settlement in the laboratory. This endeavour is worth the effort for a more realistic and accurate understanding of the complex processes in larval settlement of echinoderms.

The ability to link information on settlement processes and induction to patterns of settlement and recruitment observed in the field has been constrained by challenges to effective and accurate

sampling of echinoderm settlers, due to their extremely small size and cryptic nature. To address the limitations of conventional sampling techniques, various artificial settlement collector designs have been developed and successfully used in recent decades. The number of echinoderm studies documenting spatial and temporal settlement patterns in the field has thus markedly increased, although the majority of studies are focused on a few echinoid, asteroid and holothuroid species of ecological or economic importance. In theory, artificial collectors facilitate separation of settlement from post-settlement processes. However, this separation depends on how frequently collectors are deployed and retrieved, and in the case of unimodal annual settlement pulses, the timing of retrieval with respect to the settlement event. Because echinoderm settlers are subject to various early post-settlement processes including high mortality during the first days and weeks of their benthic life stage (Hunt & Scheibling 1997, Balch & Scheibling 2001), field studies with relatively long deployment periods are unlikely to accurately describe settlement rates, but rather relative rates of recruitment. Nevertheless, further assessments of spatiotemporal settlement patterns at appropriate scales appear critical to our understanding of the supply-side ecology of echinoderms, especially if such assessments occur in conjunction with quantitative descriptions of abiotic (e.g. temperature and hydrodynamics) and biotic factors (e.g. chlorophyll, availability of settlement substrata or conspecific aggregations) acting at the same scales. Some echinoderm studies have reported correlation of spatiotemporal settlement patterns with environmental variables, including temperature, chlorophyll concentrations and currents. However, most of these studies have failed to establish causative links with appropriate field or laboratory experiments. To explain the roles of settlement cues and processes in the natural environment, future studies on settlement patterns should thus not only aim to quantify pertinent environmental variables, but also attempt to resolve critical information gaps surrounding the links between these factors and settlement patterns observed in the field.

In brief, we argue that to meaningfully advance our understanding of echinoderm settlement, the following four directions in research should be prioritised in future studies: (1) detailed characterisation of specific chemical compounds inducing echinoderm settlement; (2) examination of biofilm-induced and bacteria-mediated settlement; (3) settlement assays testing suites of abiotic and biotic cues, replicating natural conditions as closely as possible; and (4) *in situ* quantification of settlement rates and pertinent environmental variables, with complementary experimental studies to establish causative links.

Concluding remarks

Our review of larval settlement in echinoderms has highlighted considerable spatial and temporal variability in settlement patterns across all classes (see also Balch & Scheibling 2001), although variability is much less apparent for ophiuroids. It has long been known that echinoderm larvae do not settle randomly in space and time (Ebert 1983), yet the processes and mechanisms that influence settlement patterns are highly complex and poorly understood. Settlement patterns, and the factors that influence them, are nonetheless fundamental to the population dynamics, distribution and abundance of echinoderms. Our review highlights the wide range of abiotic and biotic factors involved in the movement (locomotion and dispersal) and distribution of echinoderm larvae prior to settlement, and complex interactions between larvae and their environment throughout the settlement process. Important settlement and metamorphic cues are often associated with particular substrata or organisms that occur in benthic habitats. However, the specificity and the relative importance of settlement cues vary among classes, whereby echinoids appear to have much more generalised settlement cues, at least compared to asteroids. Further research is clearly warranted to better understand settlement in echinoderms, especially for species that are ecologically or economically important. Critically, marked fluctuations in settlement success, and thereby local abundance, of ecologically important echinoderms can have broad-scale impacts on the structure and functioning of marine ecosystems.

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References

- Agatsuma, Y., Nakao, S., Motoya, S., Tajima, K. & Miyamoto, T. 1998. Relationship between year-to-year fluctuations in recruitment of juvenile sea urchins *Strongylocentrotus nudus* and seawater temperature in Southwestern Hokkaido. *Fisheries Science* **64**, 1–5.
- Agudo, N. 2007. *Sandfish Hatchery Techniques*. Nouméa: Australian Centre for International Agricultural Research, Secretariat of the Pacific Community, the WorldFish Center.
- Allen, J.D., Richardson, E.L., Deaker, D., Agüera, A. & Byrne, M. 2019. Larval cloning in the crown-of-thorns sea star, a keystone coral predator. *Marine Ecology Progress Series* **609**, 271–276.
- Andrew, N.L. & Choat, J.H. 1985. Habitat related differences in the survivorship and growth of juvenile sea urchins. *Marine Ecology Progress Series* **27**, 155–161.
- Babcock, R.C., Mundy, C. N. & Whitehead, D. 1994. Sperm diffusion models and in situ confirmation of long-distance fertilization in the free-spawning asteroid *Acanthaster planci*. *The Biological Bulletin* **186**, 17–28.
- Bak, R.P.M. 1985. Recruitment patterns and mass mortalities in the sea urchin *Diadema antillarum*. In: *Proceedings of the Fifth International Coral Reef Congress*. Moorea: Antenne Museum-EPHE, **5**, 267–272.
- Balch, T., Hatcher, B.G. & Scheibling, R.E. 1999. A major settlement event associated with minor meteorologic and oceanographic fluctuations. *Canadian Journal of Zoology* **77**, 1657–1662.
- Balch, T. & Scheibling, R.E. 2000. Temporal and spatial variability in settlement and recruitment of echinoderms in kelp beds and barrens in Nova Scotia. *Marine Ecology Progress Series* **205**, 139–154.
- Balch, T. & Scheibling, R.E. 2001. Larval supply, settlement and recruitment in echinoderms. In: *Echinoderm Studies*, M. Jangoux & J.M. Lawrence (eds). Rotterdam/Brookfield: A. A. Balkema Publishers, 1–83.
- Balch, T., Scheibling, R.E., Harris, L.G., Chester, C.M. & Robinson, S.M.C. 1998. Variation in settlement of *Strongylocentrotus droebachiensis* in the northwest Atlantic: Effects of spatial scale and sampling method. In: *Echinoderms: San Francisco*, R. Mooi & M. Telford (eds). Rotterdam: A. A. Balkema Publishers, 555–560.
- Baloun, A.J. & Morse, D.E. 1984. Ionic control of settlement and metamorphosis in larval *Haliotis rufescens* (Gastropoda). *Biology Bulletin* **167**, 124–138.
- Balsalobre, M., Wangenstein, O.S., Palacín, C., Clemente, S. & Hernández, J.C. 2016. Efficiency of artificial collectors for quantitative assessment of sea urchin settlement rates. *Scientia Marina* **80**, 207–216.
- Balser, E.J. 1998. Cloning in ophiuroid echinoderm larvae. *The Biological Bulletin* **194**, 187–193.
- Banks, S.C., Piggott, M.P., Williamson, J.E., Bové, U., Holbrook, N.J. & Beheregaray, L.B. 2007. Oceanic variability and coastal topography shape genetic structure in a long-dispersing sea urchin. *Ecology* **88**, 3055–3064.
- Barker, M.F. 1977. Observations on the settlement of the brachiolaria larvae of *Stichaster australis* (Verrill) and *Coscinasterias calamaria* (Gray) (Echinodermata: Asteroidea) in the laboratory and on the shore. *Journal of Experimental Marine Biology and Ecology* **30**, 95–108.
- Barker, M.F. 1979. Breeding and recruitment in a population of the New Zealand starfish *Stichaster australis* (Verrill). *Journal of Experimental Marine Biology and Ecology* **41**, 195–211.
- Barker, M.F. & Nichols, D. 1983. Reproduction, recruitment and juvenile ecology of the starfish, *Asterias rubens* and *Marthasterias glacialis*. *Journal of the Marine Biological Association of the United Kingdom* **63**, 745–765.
- Basch, L.V. & Pearse, J.S. 1995. Consequences of larval feeding environment for settlement and metamorphosis of a temperate echinoderm. *Oceanologica Acta* **19**, 273–285.

- Birkeland, C. 1982. Terrestrial runoff as a cause of outbreaks of *Acanthaster planci* (Echinodermata: Asteroidea). *Marine Biology* **69**(2), 175–185.
- Birkeland, C. 1989. The influence of echinoderms on coral-reef communities. In: *Echinoderm Studies*, M. Jangoux & J.M. Lawrence (eds). Rotterdam: A. A. Balkema Publishers, 1–97.
- Birkeland, C., Chia, F.-S. & Strathmann, R.R. 1971. Development, substratum selection, delay of metamorphosis and growth in the seastar, *Mediaster aequalis* Stimpson. *The Biological Bulletin* **141**, 99–108.
- Black, K.P. & Morn, P.J. 1991. Influence of hydrodynamics on the passive dispersal and initial recruitment of *Acanthaster planci* (Echinodermata: Asteroidea) on the Great Barrier Reef. *Marine Ecology Progress Series* **69**, 55–65.
- Bode, M., Leis, J.M., Mason, L.B., Williamson, D.H., Harrison, H.B., Choukroun, S., & Jones, G.P. 2019. Successful validation of a larval dispersal model using genetic parentage data. *PLoS Biology* **17**, e3000380.
- Bonaviri, C., Gianguzza, P., Pipitone, C. & Hereu, B. 2012. Micropredation on sea urchins as a potential stabilizing process for rocky reefs. *Journal of Sea Research* **73**, 18–23.
- Bosch, I., Beauchamp, K.A., Steele, M.E. & Pearse, J.S. 1987. Development, metamorphosis, and seasonal abundance of embryos and larvae of the Antarctic sea urchin *Sterechinus neumayeri*. *The Biological Bulletin* **173**, 126–135.
- Brandhorst, B.P. & Bishop, C.D. 2001. NO/cGMP signaling and HSP90 activity represses metamorphosis in the sea urchin *Lytechinus pictus*. *The Biological Bulletin* **201**, 394–404.
- Brodie, J.K., Fabricius, K., De'ath, G. & Okaji, K. 2005. Are increased nutrient inputs responsible for more outbreaks of crown-of-thorns starfish? An appraisal of the evidence. *Marine Pollution Bulletin* **51**, 266–278.
- Brown, N.P. & Eddy, S. D. 2015. *Echinoderm aquaculture*. Hoboken: Wiley Blackwell.
- Bruno, J.F. & Selig, E.R. 2007. Regional decline of coral cover in the Indo-Pacific: Timing, extent, and sub-regional comparisons. *PLoS One* **2**, e711.
- Bryan, P.J. 2004. Energetic cost of development through metamorphosis for the starfish *Mediaster aequalis* (Stimpson). *Marine Biology* **145**, 293–302.
- Burke, R.D. 1979. Sensory structures potentially responsible for the perception of substrate associated cues to metamorphosis in echinoids. *American Zoologist* **19**, 958.
- Burke, R.D. 1980. Podial sensory receptors and the induction of metamorphosis in echinoids. *Journal of Experimental Marine Biology and Ecology* **47**, 223–234.
- Burke, R.D. 1983a. The induction of metamorphosis of marine invertebrate larvae: Stimulus and response. *Canadian Journal of Zoology* **61**, 1701–1719.
- Burke, R.D. 1983b. Neuronal control of metamorphosis in *Dendraster excentricus*. *The Biological Bulletin* **164**, 176–188.
- Burke, R.D. 1984. Phermonal control of metamorphosis in the pacific sand dollar, *Dendraster excentricus*. *Science* **225**, 442–443.
- Burke R.D. 1986. Phermones and the gregarious settlement of marine invertebrate larvae. *Bulletin of Marine Science* **39**, 323–331.
- Byrne, M. 1990. Annual reproductive cycles of the commercial sea urchin *Paracentrotus lividus* from an exposed intertidal and a sheltered subtidal habitat on the west coast of Ireland. *Marine Biology* **104**, 275–289.
- Byrne, M. 2013. Larval ecology, settlement, and recruitment of asteroids. In: *Starfish: Biology and Ecology of the Asteroidea*, J.M. Lawrence (ed.). Baltimore, Maryland: John Hopkins University Press, 51–58.
- Byrne, M. & Barker, M.F. 1991. Embryogenesis and larval development of the asteroid *Patriella regularis* viewed by light and scanning electron microscopy. *The Biological Bulletin* **180**, 332–345.
- Byrne, M., Emler, R. & Cerra, A. 2001. Ciliated band structure in planktotrophic and lecithotrophic larvae of *Heliocidaris* species (Echinodermata: Echinoidea): Conservation and change. *Acta Zoologica* **82**, 189–199.
- Byrne, M., Gall, M., Wolfe, K. & Agüera, A. 2016. From pole to pole: The potential for the Arctic seastar *Asterias amurensis* to invade a warming Southern Ocean. *Global Change Biology* **22**, 3874–3887.
- Byrne, M., Ho, M., Selvakumaraswamy, P., Nguyen, H.D., Dworjanyn, S.A. & Davis, A.R. 2009. Temperature, but not pH, compromises sea urchin fertilization and early development under near-future climate change scenarios. *Proceedings of the Royal Society B: Biological Sciences* **276**, 1883–1888.
- Byrne, M. & O'Hara, T.D. 2017. *Australian Echinoderms: Biology, Ecology & Evolution*. Melbourne: CSIRO Publishing.

- Byrne, M., Selvakumaraswamy, P., Ho, M.A., Woolsey, E. & Nguyen, H.D. 2011. Sea urchin development in a global change hotspot, potential for southerly migration of thermotolerant propagules. *Deep Sea Research Part II. Topical Studies in Oceanography* **58**, 712–719.
- Byrne, M., Sewell, M.A. & Prowse, A.A. 2008. Nutritional ecology of sea urchin larvae: Influence of endogenous and exogenous nutrition on echinopluteal growth and phenotypic plasticity in *Tripneustes gratilla*. *Functional Ecology* **22**, 643–648.
- Byrne, M., Villinski, J.T., Cisternas, P., Siegel, R.K., Popodi, E. & Raff, R.A. 1999. Maternal factors and the evolution of developmental mode: Evolution of oogenesis in *Heliocidaris erythrogramma*. *Development Genes and Evolution* **209**, 275–283.
- Caballes, C.F., Byrne, M., Messmer, V. & Pratchett, M.S. 2021. Temporal variability in gametogenesis and spawning patterns of crownofthorns starfish within the outbreak initiation zone in the northern Great Barrier Reef. *Marine Biology* **168**, 13.
- Caballes, C.F. & Pratchett, M.S. 2014. Reproductive biology and early life history of the crown-of-thorns starfish. In: *Echinoderms: Ecology, Habitats and Reproductive Biology*, E. Whitmore (ed.). New York: Nova Science Publishers, 101–146.
- Caballes, C.F. & Pratchett, M.S. 2017. Environmental and biological cues for spawning in the crown-of-thorns starfish. *PLoS One* **12**, e0173964.
- Cameron, R.A. 1975. *The Initiation and Early Events of Metamorphosis of Sea Urchins*. PhD thesis, University of California, Santa Cruz.
- Cameron, R.A., Boidon-Metairon, I. & Monterrosa O. 1985. Does the embryonic response to temperature and salinity by four species of Caribbean sea urchins parallel the reproductive synchrony? In: *Proceedings of the Fourth Coral Reef Congress*. Moorea: Antenne Museum-EPHE, **5**, 273–278.
- Cameron, R.A. & Fankboner, P.V. 1989. Reproductive biology of the commercial sea cucumber *Parastichopus californicus* (Stimpson) (Echinodermata: Holothuridea) II Observations on the ecology of development, recruitment, and juvenile life stage. *Journal of experimental Marine Biology and Ecology* **127**, 43–67.
- Cameron, R.A. & Hinegardner, R.T. 1974. Initiation of metamorphosis in laboratory cultured sea urchins. *The Biological Bulletin* **146**, 335–342.
- Cameron, R.A. & Rumrill, S.S. 1982. Larval abundance and recruitment of the aand dollar *Dendraster excentricus* in Monterey Bay, California, USA. *Marine Biology* **71**, 197–202.
- Cameron, R.A., Tosteson, T.R. & Hensely V. 1989. The control of sea urchin metamorphosis: Ionic effects. *Development Growth & Differentiation* **31**, 589–593.
- Carpenter, R.C. 1985. Sea urchin mass-mortalities: Effects on reef algal abundance, species composition, and metabolism and other reef herbivores. In: *Proceedings of the Fifth International Coral Reef Congress*. Moorea: Antenne Museum-EPHE, **4**, 53–60.
- Carpizo-Ituarte, E.J., Salas-Garza, A. & Pares-Sienna, G. 2002. Induction of metamorphosis with KCl in three species of sea urchins and its implications in the production of juveniles. *Ciencias Marinas* **28**, 157–166.
- Chesher, R.H. 1969. Destruction of Pacific corals by the sea star *Acanthaster planci*. *Science* **165**, 280–283.
- Chia, F.-S., Buckland-Nicks, J. & Young, C.M. 1984. Locomotion of marine invertebrate larvae: A review. *Canadian Journal of Zoology* **62**, 1205–1222.
- Chia, F.-S. & Burke, R.D. 1978. Echinoderm metamorphosis: Fate of larval structures. In: *Settlement and Metamorphosis of Marine Invertebrate Larvae*, F.-S. Chia & M. Rice (eds). New York: Elsevier, 219–234.
- Clemente, S., Hernández, J.C. & Brito, A. 2009. Evidence of the top – down role of predators in structuring sublittoral rocky-reef communities in a Marine Protected Area and nearby areas of the Canary Islands. *ICES Journal of Marine Science* **66**, 64–71.
- Clemente, S., Hernández, J.C., Toledo, K. & Brito, A. 2007. Predation upon *Diadema* aff. *antillarum* in barren grounds in the Canary Islands. *Scientia Marina* **71**, 745–754.
- Cowan, Z., Dworjanyn, S.A., Caballes, C.F. & Pratchett, M.S. 2016b. Benthic predators influence microhabitat preferences and settlement success of crown-of-thorns starfish (*Acanthaster* cf. *solaris*). *Diversity* **8**, 27.
- Cowan, Z., Ling, S.D., Caballes, C.F., Dworjanyn, S.A., & Pratchett, M.S. 2020. Crown-of-thorns starfish larvae are vulnerable to predation even in the presence of alternative prey. *Coral Reefs* **29**, 293–303.
- Cowan, Z., Ling, S.D., Dworjanyn, S.A., Caballes, C.F. & Pratchett, M.S. 2016a. Interspecific variation in potential importance of planktivorous damselfish as predators of *Acanthaster* sp. eggs. *Coral Reefs* **36**, 653–661.
- Cowan, Z., Pratchett, M., Messmer, V. & Ling, S. 2017. Known predators of crown-of-thorns starfish (*Acanthaster* spp.) and their role in mitigating, if not preventing, population outbreaks. *Diversity* **9**, 7.

- Crisp, D.J. 1974. Factors influencing the settlement of marine invertebrate larvae. In: *Chemoreception in Marine Organisms*, P.T. Grant & A.M. Mackie (eds). New York: Academic Press, 177–265.
- Crisp, D.J. 1979. Dispersal and re-aggregation in sessile marine invertebrates, particularly barnacles. In: *Marine Organisms – Genetics, Ecology and Evolution*, G. Larwood & B.R. Rosen (eds.). London: Academic Press, **11**, 319–327.
- Crisp, D.J. 1984. Overview of research on marine invertebrate larvae, 1940–1980. In: *Marine Biodeterioration: An Interdisciplinary Study*, J.D. Costlow & R.C. Tipper. Annapolis, Maryland: Naval Institute Press, 103–126.
- De la Uz, S., Carrasco, J.F., Rodríguez, C. & Anadón, N. 2013. Metamorphosis, growth and survival of early juveniles of *Paracentrotus lividus* (Echinodermata: Echinoidea): Effects of larval diet and settlement inducers. *Cahiers De Biologie Marine* **54**, 691–695.
- Dobretsov, S. 2010. Marine biofilms. *Biofouling* 123–136.
- Dobretsov, S. & Rittschof, D. 2020. Love at first taste: Induction of larval settlement by marine microbes. *International Journal of Molecular Science* **21**, 731.
- Doll, P.C., Messmer, V., Uthicke, S., Doyle, J.R., Caballes, C.F. & Pratchett, M.S. DNA-based detection and patterns of larval settlement of the corallivorous crown-of-thorns sea star (*Acanthaster* sp.). *The Biological Bulletin* **241**, 271–285.
- Domanski, P.A. 1984. Giant larvae: Prolonged planktonic larval phase in the asteroid *Luidia sarsi*. *Marine Biology* **80**, 189–195.
- Dworjanyn, S.A., & Pirozzi, I. 2008. Induction of settlement in the sea urchin *Tripneustes gratilla* by macroalgae, biofilms and conspecifics: A role for bacteria? *Aquaculture* **274**, 268–274.
- Ebert, T.A. 1983. Recruitment in echinoderms. In: *Echinoderm Studies*, J.M. Lawrence & M. Jangoux (eds.). Rotterdam: A. A. Balkema Publishers, 169–203.
- Ebert, T.A. 2021a. Life-history analysis of asterinid starfishes. *The Biological Bulletin* **241**, 231–242.
- Ebert, T.A. 2021b. Problems and puzzles in echinoderm demography. *Revista de Biología Tropical* **69**(Suppl. 1), 1–13.
- Ebert, T.A., Schroeter, S.C. & Dixon, J.D. 1991. Studies on the feasibility of sea urchin enhancement in California. Technical Report, No. FG9310.
- Ebert, T.A., Schroeter, S.C., Dixon, J.D. & Kalvass, P. 1994. Settlement patterns of the red and purple sea urchins (*Strongylocentrotus franciscanus* and *S. purpuratus*) in California, USA. *Marine Ecology Progress Series* **111**, 41–52.
- Emlet, R.B. 1983. Locomotion, drag, and the rigid skeleton of larval echinoderms. *The Biological Bulletin* **164**, 433–445.
- Emlet, R.B. 1988. Larval form and metamorphosis of a “primitive” sea urchin, *Euclidaris thouarsi* (Echinodermata: Echinoidea: Cidaroida), with implications for development and phylogenetic studies. *The Biological Bulletin* **174**, 4–19.
- Emlet, R.B., 1995. Developmental mode and species geographic range in regular sea urchins (Echinodermata: Echinoidea). *Evolution* **49**, 476–489.
- Emlet, R.B., McEdward, L.R. & Strathmann R.R. 1987. Echinoderm larval ecology viewed from the egg. In: *Echinoderm Studies 2*, M. Jangoux & J.M. Lawrence (eds.). Rotterdam: A. A. Balkema Publishers, 55–136.
- Endean, R. 1977. *Acanthaster planci* infestations of reefs of the Great Barrier Reef. *Proceedings of Third International Coral Reef Symposium* **1**, 185–191.
- Espinel-Velasco, N., Agüera, A. & Lamare M. 2020. Sea urchin larvae show resilience to ocean acidification at the time of settlement and metamorphosis. *Marine Environmental Research* **159**, 104977.
- Espinel-Velasco, N., Hoffmann, L., Agüera, A., Byrne A., Dupont, S., Uthicke, S., Webster, N.S. & Lamare, M. 2018. Effects of ocean acidification on the settlement and metamorphosis of marine invertebrate and fish larvae. *Marine Ecology Progress Series* **606**, 237–257.
- Estes, J.A., Terborgh, J., Brashares, J.S., Power, M.E., Berger, J., Bond, W.J., Carpenter, S.R., Essington, T.E., Holt, R.D., Jankson, J.B.C., Marquis, R.J., Oksanen, L., Oksanen, T., Paine, R.T., Pickett, E.K., Ripple, W.J., Sandin, S.A., Scheffer, M., Schoener, T.W., Shurin, J.B., Sinclair, A.R.E., Soulé, M.E., Virtanen, R. & Wardle, D.A. 2011. Trophic downgrading of planet Earth. *Science* **333**, 301–306.
- Fabricius, K.E., Okaji, K. & De'ath, G. 2010. Three lines of evidence to link outbreaks of the crown-of-thorns seastar *Acanthaster planci* to the release of larval food limitation. *Coral Reefs* **29**, 593–605.
- Falkner, I., Sewell, M.A. & Byrne, M., 2015. Evolution of maternal provisioning in ophiuroid echinoderms: Characterisation of egg composition in planktotrophic and lecithotrophic developers. *Marine Ecology Progress Series* **525**, 1–13.

- Fenaux, L., Strathmann, M.F. & Strathmann, R.R. 1994. Five tests of food-limited growth of larvae in coastal waters by comparisons of rates of development and form of echinoplutei. *Limnology and Oceanography* **39**, 84–98.
- Ferner, M.C., Hodin, J., Ng, G. & Gaylord B. 2019. Brief exposure to intense turbulence induces a sustained life-history shift in echinoids. *Journal of Experimental Biology* **222**, jeb187351.
- Flammang, P., Gosselin, P. & Jangoux, M. 1998. The podia, organs of adhesion and sensory perception in larvae and post-metamorphic stages of the echinoid *Paracentrotus lividus* (Echinodermata). *Biofouling* **12**, 161–171.
- Gage, J.D. & Tyler, P.A. 1981a. Non-viable seasonal settlement of larvae of the upper bathyal brittle star *Ophiocten gracilis* in the Rockall Trough abyssal. *Marine Biology* **64**, 153–161.
- Gage, J.D. & Tyler, P.A. 1981b. Re-appraisal of age composition, growth and survivorship of the deep-sea brittle star *Ophiura ljunghmani* from size structure in a sample time series from the Rockall Trough. *Marine Biology* **64**, 163–172.
- García, E., Hernández, J.C., Clemente, S., Cohen-Rengifo, M., Hernández, C.A. & Dupont S. 2015. Rubustness of *Paracentrotus lividus* larval and post-larval development to pH levels projected for the turn of the century. *Marine Biology* **162**, 2047–2055.
- García-Sanz, S., Navarro, P.G. & Tuya, F. 2014. Contrasting recruitment seasonality of sea urchin species in Gran Canaria, Canary Islands (eastern Atlantic). *Mediterranean Marine Science* **15**, 475–481.
- García-Sanz, S., Tuya, F., Navarro, P.G., Angulo-Preckler, C. & Haroun, R.J. 2012. Post larval, short-term, colonization patterns: The effect of substratum complexity across subtidal, adjacent, habitats. *Estuarine, Coastal and Shelf Science* **122**, 181–191.
- Gaylord, B., Hodin, J. & Ferner M.C. 2013. Turbulent shear spurs settlement in larval sea urchins. *Proceedings of the National Academy of Sciences of the United States of America* **110**, 6901–6906.
- Gilmour, J. 1999. Experimental investigation into the effects of suspended sediment on fertilisation, larval survival and settlement in a scleractinian coral. *Marine Biology* **135**, 451–462.
- Glockner-Fagetti, A. & Phillips, N.E. 2020. Species assemblage and recruitment patterns of echinoderms on shallow rocky reefs in central New Zealand. *New Zealand Journal of Marine and Freshwater Research* **54**, 286–304.
- Gosselin, P. & Jangoux, M. 1996. Induction of metamorphosis in *Paracentrotus lividus* larvae (Echinodermata, Echinoidea). *Oceanologica Acta* **19**, 293–296.
- Gosselin, P. & Jangoux, M. 1998. From competent larva to exotrophic juvenile: A morphofunctional study of the perimetamorphic period of *Paracentrotus lividus* (Echinodermata, Echinoidea). *Zoomorphology* **118**, 31–43.
- Gosselin, P. & Qian, P.-Y. 1997. Juvenile mortality in benthic marine invertebrates. *Marine Ecology Progress Series* **146**, 265–282.
- Hadfield, M.G. 1986. Settlement and recruitment of marine invertebrates: A perspective and some proposals. *Bulletin of Marine Science* **39**, 418–425.
- Hadfield, M.G. 2011. Biofilms and marine invertebrate larvae: What bacteria produce that larvae use to choose settlement sites. *Annual Review of Marine Science* **3**, 453–70.
- Hadfield, M.G., Carpizo-Ituarte, E.J., del Carmen, K. & Nedved, B.T. 2001. Metamorphic competence, a major adaptive convergence in marine invertebrate larvae. *American Zoologist* **41**, 1123–1131.
- Hadfield, M.G. & Paul, V.J. 2001. Natural chemical cues for settlement and metamorphosis of marine invertebrate larvae. In: *Marine Chemical Ecology*, J. McClintock & B. Baker (eds.). Boca Raton, Florida: CRC Press, 431–461.
- Hall, M.R., Kocot, K.M., Baughman, K.W., Fernandez-Valverde, S.L., Gauthier, M.E.A., Hatleberg, W.L., Krishnan, A., McDougall, C., Motti, C.A., Shoguchi, E., Wang, T., Xiang, X., Zhao, M., Bose, U., Shinzato, C., Hisata, K., Fujie, M., Kanda, M., Cummins, S.F., Satoh, N., Degnan, S.M. & Degnan, B.M. 2017. The crown-of-thorns starfish genome as a guide for biocontrol of this coral reef pest. *Nature* **544**, 231–234.
- Hamel, J. & Mercier, A. 1996. Early development, settlement, growth, and spatial distribution of the sea cucumber *Cucumaria frondosa* (Echinodermata: Holothuroidea). *Canadian Journal of Fisheries and Aquatic Sciences* **53**, 253–271.
- Harris, L.G., Rice, B. & Nestler, E.C. 1994. Settlement, early survival and growth in a southern Gulf of Maine population of *Strongylocentrotus droebachiensis* (Muller). In: *Echinoderms through Time*, B. David et al. (eds.). Rotterdam: A. A. Balkema Publishers, 701–706.
- Harrold, C., Lisin, S., Light, K.H. & Tudor, S. 1991. Isolating settlement from recruitment of sea urchins. *Journal of Experimental Marine Biology and Ecology* **147**, 81–94.

- Hart, M.W., Guerra, V.I., Allen, J.D. & Byrne, M. 2021. Cloning and selfing affect population genetic variation in simulations of outcrossing, sexual sea stars. *The Biological Bulletin* **241**, 286–302.
- Hart, M.W. & Scheibling, R.E. 1988. Heat waves, baby booms, and the destruction of kelp beds by sea urchins. *Marine Biology* **99**, 167–176.
- Harvell, C.D., Montecino-Latorre, D., Caldwell, J.M., Burt, J.M., Bosley, K., Keller, A., Heron, S.F., Salomon, A.K., Lee, L., Pontier, O., Pattengill-Semmens, C. & Gaydos, J.K. 2019. Disease epidemic and a marine heat wave associated with the continental-scale collapse of a pivotal predator (*Pycnopodia helianthoides*). *Science Advances* **5**, eaau7042.
- Henderson, J.A. & Lucas, J.S. 1971. Larval development and metamorphosis of *Acanthaster planci* (Asteroidea). *Nature* **232**, 655–657.
- Hendler, G. 1991. Echinodermata: Ophiuroidea. In: *Reproduction of Marine Invertebrates: Echinoderms and Lophophorates*, A.C. Giese et al. (eds.). Pacific Grove, California: The Boxwood Press, 356–511.
- Hentschel, B.T. 1999. Complex life cycles in a variable environment: Predicting when the timing of metamorphosis shifts from resource dependent to developmentally fixed. *American Naturalist* **154**, 549–558.
- Hereu, B., Zabala, M., Linares, C. & Sala, E. 2004. Temporal and spatial variability in settlement of the sea urchin *Paracentrotus lividus* in the NW Mediterranean. *Marine Biology* **144**, 1011–1018.
- Hereu, B., Zabala, M., Linares, C. & Sala, E. 2005. The effects of predator abundance and habitat structural complexity on survival of juvenile sea urchins. *Marine Biology* **146**, 293–299.
- Hernández, J.C., Brito, A., Cubero, E., Nayra, G., Girard, D., González-Lorenzo, G. & Falcón, J.M. 2006. Temporal patterns of larval settlement of *Diadema antillarum* (Echinodermata: Echinoidea) in the Canary Islands using an experimental larval collector. *Bulletin of Marine Science* **78**, 271–279.
- Hernández, J.C., Clemente, S., Girard, D., Pérez-Ruzafa, Á. & Brito, A. 2010. Effect of temperature on settlement and post-settlement survival in a barren-forming sea urchin. *Marine Ecology Progress Series* **413**, 69–80.
- Heyland, A. & Hodin, J. 2004. Heterochronic developmental shift caused by thyroid hormone in larval sand dollars and its implications for phenotypic plasticity and the evolution of nonfeeding development. *Evolution* **58**, 524–538.
- Heyland, A., Reitzel, A.M. & Hodin, J. 2004. Thyroid hormones determine developmental mode in sand dollars (Echinodermata, Echinoidea). *Evolution and Development* **6**, 382–389.
- Heyland, A., Reitzel, A.M., Price, D. & Moroz, L.L. 2006. Endogenous thyroid hormone synthesis in facultative planktotrophic larvae of the sand dollar *Clypeaster rosaceus*, implications from the evolutionary loss of larval feeding. *Evolution & Development* **8**, 568–579.
- Highsmith, R.C. 1982. Induced settlement and metamorphosis of sand dollar (*Dendraster excentricus*) larvae in predator-free sites: Adult sand dollar beds. *Ecology* **63**, 329–337.
- Highsmith, R.C. & Emlet, R.B. 1986. Delayed metamorphosis, effect on growth and survival of juvenile sand dollars (Echinoidea, Clypeasteroidea). *Bulletin of Marine Science* **39**, 347–361.
- Hirata, K.Y. & Hadfield, M.G. 1986. The role of choline in metamorphic induction of *Phestilla* (Gastropoda, Nudibranchia). *Comparative Biochemistry and Physiology* **84**, 15–21.
- Hock, K., Wolff, N.H., Condie, S. A., Anthony, K.R. & Mumby, P.J. 2014. Connectivity networks reveal the risks of crown-of-thorns starfish outbreaks on the Great Barrier Reef. *Journal of Applied Ecology* **51**, 1188–1196.
- Hodin, J., Ferner, M.C. & Gaylord, B. 2020. Choosing the right home: Settlement responses by larvae of six sea urchin species align with hydrodynamic traits of their contrasting adult habitats. *Zoological Journal of the Linnean Society* **190**, 737–756.
- Hodin, J., Ferner, M.C., Ng, G. & Gaylord, B. 2018. Sand dollar larvae show within-population variation in their settlement induction by turbulence. *The Biological Bulletin* **235**, 152–166.
- Hodin, J., Ferner, M.C., Ng, G., Lowe, C.J. & Gaylord, B. 2015. Rethinking competence in marine life cycles: Ontogenetic changes in the settlement response of sand dollar larvae exposed to turbulence. *Royal Society Open Science* **2**, 150114.
- Hodin, J., Heyland, A., Mercier, A., Pernet, B., Cohen, D.L., Hamel, J.-F., Allen, J.D., McAlister, J.S., Byrne, M., Cisternas, P. & George, S.B. 2019. Culturing echinoderm larvae through metamorphosis. In: *Echinoderms, Part A. Methods in Cell Biology*, K.R. Foltz & A. Hamoun (eds.). New York: Elsevier, **150**, 125–169.
- Houlihan, E.P., Espinel-Velasco, N., Cornwall, C.E., Pilditch, C.A., & Lamare, M.D. 2020. Diffusive boundary layers and ocean acidification: Implications for sea urchin settlement and growth. *Frontiers in Marine Science* **7**, 972.

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- Huggett, M.J., Williamson J.E., de Nys, R., Kjelleberg, S. & Steinberg, P.D. 2006. Larval settlement of the common Australian sea urchin *Heliocidaris erythrogramma* in response to bacteria from the surface of coralline algae. *Oecologia* **149**, 604–619.
- Hughes, T.P., Keller, B.D., Jackson, J.B.C. & Boyle, M.J. 1985. Mass mortality of the echinoid *Diadema antillarum* Philippi in Jamaica. *Bulletin of Marine Science* **36**, 377–384.
- Hunt, H.L. & Scheibling, R.E. 1997. Role of early post-settlement mortality in recruitment of benthic marine invertebrates. *Marine Ecology Progress Series* **155**, 269–301.
- Hunte, W. & Younglao, D. 1988. Recruitment and population recovery of *Diadema antillarum* (Echinodermata: Echinoidea) in Barbados. *Marine Ecology Progress Series* **45**, 109–119.
- Ito, S. & Kitamura, H. 1997. Induction of larval metamorphosis in the sea cucumber *Stichopus japonicus* by periphytic diatoms. *Hydrobiologia* **358**, 281–284.
- Jennings, L.B. & Hunt, H.L. 2010. Settlement, recruitment and potential predators and competitors of juvenile echinoderms in the rocky subtidal zone. *Marine Biology* **157**, 307–316.
- Johnson, C.R. & Sutton, D.C. 1994. Bacteria on the surface of crustose coralline algae induce metamorphosis of the crown-of-thorns starfish *Acanthaster planci*. *Marine Biology* **120**, 305–310.
- Johnson, C.R., Sutton, D.C., Olson, R.R. & Giddins, R. 1991. Settlement of crown-of-thorns starfish: Role of bacteria on surfaces of coralline algae and a hypothesis for deep-water recruitment. *Marine Ecology Progress Series* **71**, 143–162.
- Juinio-Meñez, M.A. & Bangi, H.G.P. 2010. Extrinsic and intrinsic factors affecting the metamorphic rate of *Triploneustes gratilla* (Echinodermata: Echinoidea). *Marine Ecology Progress Series* **402**, 137–145.
- Kamya, P.Z., Dworjanyn, S.A., Hardy, N., Mos, B., Uthicke, S. & Byrne, M. 2014. Larvae of the coral eating crown-of-thorns starfish, *Acanthaster planci* in a warmer-high CO₂ ocean. *Global Change Biology* **20**, 3365–3376.
- Kay, S.W.C., Gehman, A.-L.M. & Harley, C.D.G. 2019. Reciprocal abundance shifts of the intertidal sea stars, *Evasterias troschelii* and *Pisaster ochraceus*, following sea star wasting disease. *Proceedings of the Royal Society B: Biological Sciences* **286**, 2182766.
- Kayal, M., Vercelloni, J., De Loma, T.L., Bosserelle, P., Chancerelle, Y., Geoffroy, S., Stievenart, C., Michonneau, F., Penin, L., Planes, S. & Adjeroud, M., 2012. Predator crown-of-thorns starfish (*Acanthaster planci*) outbreak, mass mortality of corals, and cascading effects on reef fish and benthic communities. *PLoS One* **7**, e47363.
- Keesing, J.K., Cartwright, C.M. & Hall, K.C. 1993. Measuring settlement intensity of echinoderms on coral reefs. *Marine Biology* **117**, 399–407.
- Keesing, J.K. & Halford, A.R. 1992. Importance of post-settlement processes for the population dynamics of *Acanthaster planci* (L.). *Australian Journal of Marine and Freshwater Research* **43**, 635–651.
- Keesing, J.K., Halford, A.R. & Hall, K.C. 2018. Mortality rates of small juvenile crown-of-thorns starfish *Acanthaster planci* on the Great Barrier Reef: Implications for population size and larval settlement thresholds for outbreaks. *Marine Ecology Progress Series* **597**, 179–190.
- Kelly, M.S. 2005. Echinoderms: their culture and bioactive compounds. In: *Progress in Molecular and Subcellular Biology: Subseries Marine Molecular Biotechnology*, V. Matranga (ed.). Berlin/Heidelberg: Springer-Verlag, 139–165.
- Kitamura, H., Kitahara, S. & Hirayamam, K. 1992. Lipophilic inducers extracted from *Corallina pilulifera* for larval settlement and metamorphosis of two sea urchins *Pseudocentrotus depressus* and *Anthocidaris crassispina*. *Nippon Suisan Gakkaishi* **58**, 75–78.
- Kitamura, H., Kitahara, S. & Koh, H.B. 1993. The induction of larval settlement and metamorphosis of two sea urchins, *Pseudocentrotus depressus* and *Anthocidaris crassispina*, by free fatty acids extracted from the coralline red alga *Corallina pilulifera*. *Marine Biology* **115**, 387–392.
- Kitamura, H., Kitahara, S. & Koh, H.B. 1994. Induction of larval settlement and metamorphosis in the sea urchins *Pseudocentrotus depressus* and *Anthocidaris crassispina* by fatty acids. *Fisheries Science* **60**, 311–313.
- Kitazawa, C., Akahoshi, S., Sohara, S., Noh, J.T., Tajika, A., Yamanaka, A. & Komatsu, M. 2015. Development of the brittle star *Ophiothrix exigua* Lyman, 1874 a species that bypasses early unique and typical planktotrophic ophiopluteus stages. *Zoomorphology* **134**, 93–105.
- Komatsu, M., Sewell, M., Carson, S.F. & Chia, F.-S. 2000. Larval development and metamorphosis of the sea star *Luidia foliolata* (Echinodermata: Asteroidea). *Species Diversity* **5**, 155–162.
- Künitzer, A. 1989. Factors affecting population dynamics of *Amphiura filiformis* (Echinodermata: Ophiuroidea) and *Mysella bidentate* (Bivalvia: Galeommatacea) in the North Sea. In: *Reproduction, Genetics and Distributions of Marine Organisms*, J.S. Ryland & P.A. Tyler (eds). Fredensborg: Olsen and Olsen, 395–406.

- Lahaye, M.C. & Jangoux, M. 1985. Post-spawning behaviour and early development of the comatulid ctenoid, *Antedon bifida*. In: *Proceedings of the Fifth International Echinoderm Conference, Galway*, B.F. Keegan & B.D.S. O'Connor (eds). Rotterdam: A. A. Balkema Publishers, 181–184.
- Lamare, M.D. & Barker, M.F. 1999. *In situ* estimates of larval development and mortality in the New Zealand sea urchin *Evechinus chloroticus* (Echinodermata: Echinoidea). *Marine Ecology Progress Series* **180**, 197–211.
- Lamare, M.D. & Barker, M.F. 2001. Settlement and recruitment of the New Zealand sea urchin *Evechinus chloroticus*. *Marine Ecology Progress Series* **218**, 153–166.
- Lambert, D.M. & Harris, L.G. 2000. Larval settlement of the green sea urchin, *Strongylocentrotus droebachiensis*, in the southern Gulf of Maine. *Invertebrate Biology* **119**, 403–409.
- Lessios, H.A. 1988. Population dynamics of *Diadema antillarum* (Echinodermata: Echinoidea) following mass mortality in Panama. *Marine Biology* **95**, 515–526.
- Lessios, H.A., Cubitt, J.D., Robertson, D.R., Shulman, M.J., Parker, M.R., Garrity, S.D. & Levings, S.C. 1984. Mass mortality of *Diadema antillarum* on the Caribbean coast of Panama. *Coral Reefs* **3**, 173–182.
- Lewin, R. 1986. Supply-side ecology. *Science* **234**, 25–27.
- Li, L., Li, Q. & Kong, L. 2011b. Effects of environmental factors on larval settlement of sea cucumber, *Apostichopus japonicus* (Selanka). *Journal of the World Aquaculture Society* **41**, 936–941.
- Li, L., Li, Q., Sun, X. & Kong, L. 2011a. Effects of temperature and salinity on larval growth, survival, and development of the sea cucumber *Apostichopus japonicus*. *North American Journal of Aquaculture* **73**, 296–303.
- Ling, S.D. & Johnson, C.R. 2009. Native spider crab causes high incidence of sub-lethal injury to the introduced seastar *Asterias amurensis*. In *Proceedings of the 13th International Echinoderm Conference, Hobart*, 5–9.
- Ling, S.D. & Johnson, C.R. 2012. Marine reserves reduce risk of climate-driven phase shift by reinstating size- and habitat-specific trophic interactions. *Ecological Applications* **22**, 1232–1245.
- Ling, S.D., Johnson, C.R., Frusher, S.D. & Ridgway, K.R. 2009. Overfishing reduces resilience of kelp beds to climate-driven catastrophic phase shift. *Proceedings of the National Academy of Sciences* **106**, 22341–22345.
- Ling, S.D., Johnson, C.R., Frusher, S. & King, C.K. 2008. Reproductive potential of a marine ecosystem engineer at the edge of a newly expanded range. *Global Change Biology* **14**, 907–915.
- Ling, S.D., Johnson, C.R., Ridgway, K., Hobday, A.J. & Haddon, M. 2009. Climate-driven range extension of a sea urchin: Inferring future trends by analysis of recent population dynamics. *Global Change Biology* **15**, 719–731.
- Ling, S.D., Kriegisch, N., Woolley, B. & Reeves, S.E., 2019. Density-dependent feedbacks, hysteresis, and demography of overgrazing sea urchins. *Ecology* **100**, e02577.
- Ling, S.D., Scheibling, R.E., Rassweiler, A., Johnson, C.R., Shears, N., Connell, S.D., Salomon, A.K., Norderhaug, K.M., Pérez-Matus, A., Hernández, J.C., Clemente, S., Blamey, L.K., Hereu, B., Ballesteros, E., Sala, E., Garrabou, J., Cebrian, E., Zabala, M., Fujita, D. & Johnson, L.E. 2015. Global regime shift dynamics of catastrophic sea urchin overgrazing. *Philosophical Transactions of the Royal Society B: Biological Sciences* **370**, 2013269.
- Loosanoff, V.L. 1964. Variations in time and intensity of setting of the starfish, *Asterias forbesi*, in Long Island sound during a twenty-five-year period. *The Biological Bulletin* **126**, 423–439.
- López, S., Turon, X., Montero, E., Palacín, C., Duarte, C.M. & Tarjuelo, I. 1998. Larval abundance, recruitment and early mortality in *Paracentrotus lividus* (Echinoidea). Interannual variability and plankton-benthos coupling. *Marine Ecology Progress Series* **172**, 239–251.
- Lucas, J.S. 1973. Reproductive and larval biology of *Acanthaster planci* (L.) in Great Barrier Reef waters. *Micronesica* **9**, 197–203.
- Lucas, J.S. 1974. Environmental influences on the early development of *Acanthaster planci* (L.). In: *Crown-of-thorns starfish Seminar Proceedings, Brisbane*. Canberra: Australian Government Publishing Service, 109–121.
- Lucas, J.S. 1982. Quantitative studies of feeding and nutrition during larval development of the coral reef asteroid *Acanthaster planci* (L.). *Journal of Experimental Marine Biology and Ecology* **65**, 173–193.
- Maldonado-Sánchez, J., Mariño-Tapia, I., Herrera-Dorantes, M.T. & Ardisson, P.-L. 2019. Hydrodynamic conditions that favor the settlement of *Diadema antillarum* to a western Caribbean coral reef. *Bulletin of Marine Science* **95**, 251–264.

- Marconi, L.J., Stivale, A., Shah, M.A. & Shelley, C. 2019. Light-dependent electrical activity in sea urchin tube feet cells. *The Biological Bulletin* **236**, 108–114.
- Marshall, D.J. & Keough, M.J. 2003. Variation in the dispersal potential of non-feeding invertebrate larvae: The desperate larva hypothesis and larval size. *Marine Ecology Progress Series* **255**, 145–153.
- Matsuura, H., Yazaki, I. & Okino, T. 2009. Induction of larval metamorphosis in the sea cucumber *Apostichopus japonicus* by neurotransmitters. *Fisheries Science* **75**, 777–783.
- Mazur, J.E. & Miller J.W. 1971. A description of the complete metamorphosis of the sea urchin *Lytechinus Variegatus* cultured in synthetic sea water. *The Ohio Journal of Science* **71**, 30–36.
- McCallum, H.I. 1987. Predator regulation of *Acanthaster planci*. *Journal of Theoretical Biology* **127**, 207–220.
- McClanahan, T.R. 1988. Coexistence in a sea urchin guild and its implications to coral reef diversity and degradation. *Oecologia* **77**, 210–218.
- McClanahan, T.R. & Muthiga, N.A. 1989. Patterns of predation of a sea urchin, *Echinometra mathaei* (de Blainville), on Kenyan coral reefs. *Journal of Experimental Marine Biology and Ecology* **126**, 77–94.
- McEdward, L.R. 1984. *On Growth and Form of Echinoplutei*. PhD thesis, University of Washington, Seattle.
- McEdward, L.R. & Chia, F.S., 1991. Size and energy content of eggs from echinoderms with pelagic lecithotrophic development. *Journal of Experimental Marine Biology and Ecology* **147**, 95–102.
- McEdward, L.R. & Miner, B.G. 2001. Larval and life-cycle patterns in echinoderms. *Canadian Journal of Zoology* **79**, 1125–1170.
- McEdward, L.R. & Miner, B.G. 2007. Echinoid larval ecology. In: *Edible Sea Urchins: Biology & Ecology*. J.M. Lawrence (ed.). Amsterdam: Elsevier Science, 71–93.
- McEuen, F.S. 1986. *The Reproductive Biology and Development of Twelve Species of Holothuroids from the San Juan Islands, Washington*. PhD thesis, University of Alberta, Edmonton, Canada.
- McEuen, F.S. & Chia, F.-S. 1985. Larval development of a molpadiid holothuroid, *Molpadia intermedia* (Ludwig, 1894) (Echinodermata). *Canadian Journal of Zoology* **63**, 2553–2559.
- Mellin, C., Matthews, S., Anthony, K.R., Brown, S.C., Caley, M.J., Johns, K.A., Osborne, K., Puotinen, M., Thompson, A., Wolff, N.H. & Fordham, D.A. 2019. Spatial resilience of the Great Barrier Reef under cumulative disturbance impacts. *Global Change Biology* **25**, 2431–2445.
- Menge, B.A., Cerny-Chipman, E.B., Johnson, A., Sullivan, J., Gravem, S. & Chan, F. 2016. Sea star wasting disease in the keystone predator *Pisaster ochraceus* in Oregon: Insights into differential population impacts, recovery, predation rate, and temperature effects from long-term research. *PLoS One* **11**, e0153994.
- Mercier, A., Battaglene, S.C. & Hamel, J. 2000. Settlement preferences and early migration of the tropical sea cucumber *Holothria scabra*. *Journal of Experimental Marine Biology and Ecology* **249**, 89–110.
- Metaxas, A. 2013. Larval ecology, settlement, and recruitment of asteroids. In: *Starfish: Biology and Ecology of the Asteroidea*, J.M. Lawrence (ed.). Baltimore, Maryland: John Hopkins University Press, 59–66.
- Metaxas, A. 2020. Larval ecology of echinoids. In: *Sea Urchins: Biology and Ecology*, J.M. Lawrence (ed.). Amsterdam: Elsevier Science, 77–93.
- Metaxas, A., Scheibling, R.E., Robinson, M.C. & Young, C.M. 2008. Larval development, settlement, and early post-settlement behaviour of the tropical sea star *Oreaster reticulatus*. *Bulletin of Marine Science* **83**, 471–480.
- Miller, B.A. & Emllet, R.B. 1997. Influence of nearshore hydrodynamics on larval abundance and settlement of sea urchins *Strongylocentrotus franciscanus* and *S. purpuratus* in the Oregon upwelling zone. *Marine Ecology Progress Series* **148**, 83–94.
- Miller, M.W., Kramer, K.L., Williams, S.M., Johnston, L. & Szmant, A.M. 2009. Assessment of current rates of *Diadema antillarum* larval settlement. *Coral Reefs* **28**, 511–515.
- Mladenov, P.V. & Chia, F.S. 1983. Development, settling behaviour, metamorphosis and pentacrinoid feeding and growth of the feather star, *Florometra serratissima*. *Marine Biology* **73**, 309–323.
- Montgomery, E.M., Hamel, J.F. & Mercier, A. 2017. Ontogenetic shifts in swimming capacity of echinoderm propagules: A comparison of species with planktotrophic and lecithotrophic larvae. *Marine Biology* **164**, 43.
- Morgan, R. & Jangoux, M. 2004. Reproductive cycle and spawning induction in the gregarious brittle-star *Ophiothrix fragilis* (Echinodermata) in the Oosterschelde (Netherlands). *Invertebrate Reproduction & Development* **42**, 145–155.
- Morgan, R. & Jangoux, M. 2005. Larval morphometrics and influence of adults on settlement in the gregarious ophiuroid *Ophiothrix fragilis* (Echinodermata). *The Biological Bulletin* **208**, 92–99.
- Mos, B., Byrne, M. & Dworjanyn, S.A. 2020. Effects of low and high pH on sea urchin settlement, implications for the use of alkali to counter the impacts of acidification. *Aquaculture* **528**, 735618.

- Mos, B., Cowden, K.L., Nielsen, S.J. & Dworjanyn, S.A. 2011. Do cues matter? Highly inductive settlement cues don't ensure high post-settlement survival in sea urchin aquaculture. *PLoS One* **6**, e28054.
- Mos, B. & Dworjanyn, S.A. 2016. Early metamorphosis is costly and avoided by young, but physiologically competent, marine larvae. *Marine Ecology Progress Series* **559**, 117–129.
- Motti, C.A., Bose, U., Roberts, R.E., McDougall, C., Smith, M.K., Hall, M.R. & Cummings, S.F. 2018. Chemical ecology of chemosensation in asteroidea: Insights towards management strategies of pest species. *Journal of Chemical Ecology* **44**, 146–177.
- Muus, K. 1981. Density and growth of juvenile *Amphiura filiformis* (Ophiuroidea) in the Oresund. *Ophelia* **20**, 153–168.
- Naidenko, T.K. 1996. Induction of metamorphosis of two species of sea urchin from Sea of Japan. *Marine Biology* **126**, 685–692.
- Nelson, K.S., Baltar, F., Lamare, M.D. & Morales, S.E. 2020. Ocean acidification affects microbial community and invertebrate settlement on biofilms. *Scientific Reports* **10**, 3274.
- Nelson, W.G. 1979. Observations on the settlement patterns of *Janua (Dexiospira) brasiliensis* (Polychaeta: Serpulidae). *Estuaries* **2**, 213–217.
- Nontunha, N., Chaiyamon, A., Chaichotranunt, S., Tinikul, R., Poomtong, T., Sobhon, P. & Tinikul, Y. 2021. Neurotransmitters induce larval settlement and juvenile growth of the sea cucumber, *Holothuria scabra*. *Aquaculture* **535**, 736427.
- Nunes, C.D.A.P. & Jangoux, M. 2008. Induction of larval metamorphosis, survival and growth of early juveniles if the borrowing echinoid *Echinocardium cordatum* (Echinodermata). *Cahiers de Biologie Marine* **49**, 175–184.
- Obuchi, M., Fujita, Y., Nakano, Y., Uehara, T. & Motokawa, T. 2010. Reproductive biology and early life history of the hermaphroditic feather star *Dorometra sesokonis* (Echinodermata: Crinoidea). *Marine Biology* **157**, 1191–1201.
- O'Connor, B., Bowmer, T. & Grehan, A. 1983. Long-term assessment of the population dynamics of *Amphiura filiformis* (Echinodermata: Ophiuroidea) in Galway Bay (west coast of Ireland). *Marine Biology* **75**, 279–286.
- Okamoto, D.K., Schroeter, S.C. & Reed, D.C. 2020. Effects of ocean climate on spatiotemporal variation in sea urchin settlement and recruitment. *Limnology and Oceanography* **65**, 2076–2091.
- Ormond, R.F.G. & Campbell, A.C. 1974. Formation and breakdown of *Acanthaster planci* aggregations in the Red Sea. *Proceedings of the Second International Coral Reef Symposium* **1**, 595–619.
- Paine, R.T. 1969. The *Pisaster-Tegula* interaction: Prey patches, predator food preference, and intertidal community structure. *Ecology* **50**(6), 950–961.
- Pawlik, J.R. 1992. Chemical ecology of the settlement of benthic marine invertebrates. *Oceanography and Marine Biology: An Annual Review* **30**, 273–335.
- Pawlik, J.R. & Faulkner, D.J. 1986. Specific free fatty acids induce larval settlement and metamorphosis of the reef-building tube worm *Phragmatopoma californica* (Fewkes). *Journal of Experimental Marine Biology and Ecology* **102**, 301–310.
- Pawson, D.L. 2007. Phylum echinodermata. *Zootaxa* **1668**, 749–764.
- Pearce, C.M. 1997. Induction of settlement and metamorphosis in echinoderms. In *Recent Advances in Marine Biotechnology. Vol 1 Endocrinology and Reproduction*, M. Fingerman et al. (eds.). New Delhi: Oxford & IBH Publishing, 283–341.
- Pearce, C.M. & Scheibling, R.E. 1990a. Induction of settlement and metamorphosis in the sand dollar *Echinarachnius parma*: Evidence for an adult-associated factor. *Marine Biology* **107**, 363–369.
- Pearce, C.M. & Scheibling, R.E. 1990b. Induction of metamorphosis of larvae of the green sea urchin, *Strongylocentrotus droebachiensis*, by coralline red algae. *The Biological Bulletin* **179**, 304–311.
- Pearce, C.M. & Scheibling, R.E. 1991. Effect of macroalgae, microbial films, and conspecifics on the induction of metamorphosis of the green sea urchin *Strongylocentrotus droebachiensis* (Müller). *Journal of Experimental Marine Biology and Ecology* **147**, 147–162.
- Pearce, C.M. & Scheibling, R.E. 1994. Induction of metamorphosis of larval echinoids (*Strongylocentrotus droebachiensis* and *Echinarachnius parma*) by potassium chloride (KCl). *Invertebrate Reproduction and Development* **26**, 213–220.
- Pearse, J.S. & Cameron, R.A. 1991. Echinodermata: Echinoidea. In: *Reproduction of Marine Invertebrates Vol. 6 Echinoderms and Lophophorates*, A.C. Giese et al. (eds). Pacific Grove, California: The Boxwood Press, 513–662.

- Pederson, H.G. & Johnson, C.R. 2006. Predation of the sea urchin *Heliocidaris erythrogramma* by rock lobsters (*Jasus edwardsii*) in no-take marine reserves. *Journal of Experimental Marine Biology and Ecology* **336**, 120–134.
- Phillips, N.E. & Shima J.S. 2006. Differential effects of suspended sediments on larval survival and settlement of New Zealand urchins *Evechinus chloroticus* and abalone *Haliotis iris*. *Marine Ecology Progress Series* **314**, 149–158.
- Pratchett, M.S., Caballes, C.F., Rivera-Posada, J.A. & Sweatman, H.P.A. 2014. Limits to understanding and managing outbreaks of crown-of-thorns starfish (*Acanthaster* spp.). *Oceanography and Marine Biology: An Annual Review* **52**, 133–200.
- Pratchett, M.S., Dworjanyn, S.A., Mos, B., Caballes, C.F., Thompson, C.A. & Blowes, S. 2017. Larval survivorship and settlement of crown-of-thorns starfish (*Acanthaster* cf. *solaris*) at varying algal cell densities. *Diversity* **9**, 2.
- Privitera, D., Noli, M., Falugi, C. & Chiantore, M. 2011. Benthic assemblages and temperature effects on *Paracentrotus lividus* and *Arbacia lixularvae* and settlement. *Journal of Experimental Marine Biology and Ecology* **407**, 6–11.
- Purcell, S.W., Conand, C., Uthicke, S. & Byrne M. 2016. Ecological roles of exploited sea cucumbers. *Oceanography and Marine Biology: An Annual Review* **54**, 367–386.
- Raff, R.A. & Byrne, M. 2006. The active evolutionary lives of echinoderm larvae. *Heredity* **97**, 244–252.
- Rahim, S.A.K.A., Li, J.-Y. & Kitamura, H. 2004. Larval metamorphosis of the sea urchins, *Pseudocentrotus depressus* and *Anthocidaris crassispina* in response to microbial films. *Marine Biology* **144**, 71–78.
- Rahman, M.A. & Uehara, T. 2001. Induction of metamorphosis and substratum preference in four sympatric and closely related species of sea urchins (genus *Echinometra*) in Okinawa. *Zoological Studies* **40**, 29–43.
- Raimondi, P.T., Barnett, A.M. & Krause, P.R. 1997. The effects of drilling muds on marine invertebrate larvae and adults. *Environmental Toxicology and Chemistry* **16**, 1218–1228.
- Rodríguez, S.R., Ojeda, F.P. & Inestrosa, N.C. 1993. Settlement of benthic marine invertebrates. *Marine Ecology Progress Series* **97**, 193–207.
- Rogers, A. & Lorenzen, K. 2016. Does slow and variable recovery of *Diadema antillarum* on Caribbean fore-reefs reflect density-dependent habitat selection? *Frontiers in Marine Science* **3**, 63.
- Rowley, R.J. 1989. Settlement and recruitment of sea urchins (*Strongylocentrotus* spp.) in a sea-urchin barren ground and a kelp bed: Are populations regulated by settlement or post-settlement processes? *Marine Biology* **100**, 485–494.
- Rowley, R.J. 1990. Newly settled sea urchins in a kelp bed and urchin barren ground: A comparison of growth and mortality. *Marine Ecology Progress Series* **62**, 229–240.
- Rumrill, S.S. 1987. *Differential Predation upon Embryos and Larvae of Temperate Pacific Echinoderms*. PhD thesis. University of Alberta, Edmonton, Canada.
- Rumrill, S.S. 1990. Natural mortality of marine invertebrate larvae. *Ophelia* **32**, 163–198.
- Rumrill, S.S. & Chia, F.-S. 1985. Differential mortality during the embryonic and larval lives of northeast Pacific echinoids. In: *Echinodermata*, B.F. Keegan & B.D.S. O'Connor (eds). Rotterdam: A. A. Balkema Publishers, 333–338.
- Sala, E., Boudouresque, C.F. & Harmelin-Vivien, M. 1998. Fishing, trophic cascades, and the structure of algal assemblages: Evaluation of an old but untested paradigm. *Oikos* **82**, 425–439.
- Sala, E. & Zabala, M. 1996. Fish predation and the structure of the sea urchin *Paracentrotus lividus* populations in the NW Mediterranean. *Marine Ecology Progress Series* **140**, 71–81.
- Scheibling, R.E. & Hatcher, B.G. 2007. The ecology of *Strongylocentrotus droebachiensis*. Edible sea urchins: Biology and ecology. In: *Developments in Aquaculture and Fisheries Science No. 37*, J.M. Lawrence (ed.). Amsterdam: Elsevier Science, 353–382.
- Scheibling, R.E. & Robinson M.C. 2008. Settlement behaviour and early post-settlement predation of the sea urchin *Strongylocentrotus droebachiensis*. *Journal of Experimental Marine Biology and Ecology* **365**, 59–66.
- Scheltema, R.S. 1974. Biological interactions determining larval settlement of marine invertebrates. *Thalassia Jugoslavica* **10**, 263–269.
- Schroeter, S.C., Dixon, J.D., Ebert T.A. & Rankin J.V. 1996. Effects of kelp forests *Macrocystis pyrifera* on the larval distribution and settlement of red and purple sea urchins *Strongylocentrotus franciscanus* and *S. purpuratus*. *Marine Ecology Progress Series* **133**, 125–134.
- Schultz, J.A., Cloutier, R.N. & Côté, I.M. 2016. Evidence for a trophic cascade on rocky reefs following sea star mass mortality in British Columbia. *PeerJ* **4**, e1980.

- Selvakumaraswamy, P. & Byrne, M. 2004. Metamorphosis and developmental evolution in *Ophionereis* (Echinodermata: Ophiuroidea). *Marine Biology* **145**, 87–99.
- Selvakumaraswamy, P. & Byrne, M. 2006. Evolution of larval form in ophiuroids: Insights from the metamorphic phenotype of *Ophiothrix* (Echinodermata: Ophiuroidea). *Evolution & Development* **8**, 183–190.
- Sewell, M.A. 1994. Birth, recruitment and juvenile growth in the intraovarian brooding sea cucumber *Leptosynapta clarki*. *Marine Ecology Progress Series* **114**, 149–156.
- Sewell, M.A. & Watson, J.C. 1993. A 'source' for asteroid larvae?: Recruitment of *Pisaster ochraceus*, *Pycnopodia helianthoides* and *Dermasterias imbricata* in Nootka Sound, British Columbia. *Marine Biology* **117**, 387–198.
- Slattery, M. 1997. Chemical cues in marine invertebrate larval settlement. In: *Marine Woodboring and Fouling Organisms of the Indian Ocean: A Review*, R. Nagabhushanam & J.F. Thompson (eds.). New Delhi: Oxford and IBH Publishing Co.
- Smith, M.M., Cruz Smith, L., Cameron, R.A. & Urry, L.A. 2008. The larval stages of the sea urchin, *Strongylocentrotus purpuratus*. *Journal of Morphology* **269**, 713–733.
- Sotelo-Casas, R.C., Cupul-Magaña, A.L., Solís-Marín, F.A. & Rodríguez-Troncoso, A.P. 2016. Recruitment patterns of 2 sea cucumber species in a Central Mexican Pacific coral reef community. *Revista Mexicana de Biodiversidad* **87**, 86–91.
- Steinberg, P.D., de Nys, R. & Kjelleberg, S. 2001. Chemical mediation of surface colonization. In: *Marine Chemical Ecology*, J.B. McClintock & B.J. Baker (eds). Boca Raton, Florida: CRC Press, 355–387.
- Steneck, R.S., Graham, M.H., Bourque, B.J., Corbett, D., Erlandson, J.M., Estes, A. & Tegner, M.J. 2002. Kelp forest ecosystems: Biodiversity, stability, resilience and future. *Environmental Conservation* **29**, 436–459.
- Strathmann, M.F. 1987. *Reproduction and Larval Development of Marine Invertebrates of the Northern Pacific Coast*. Seattle, Washington: University of Washington Press.
- Strathmann, R.R. 1978. Larval settlement in echinoderms. In: *Settlement and Metamorphosis of Marine Invertebrate Larvae*, F.-S. Chia & M.E. Rice (eds). New York: Elsevier, 235–246.
- Sumida, P.Y.G., Tyler, P.A., Lampitt, R.S. & Gage, J.D. 2000. Reproduction, dispersal and settlement of the bathyal ophiuroid *Ophiocten gracilis* in the NE Atlantic Ocean. *Marine Biology* **137**, 623–630.
- Sun, X., Li, Q., Yu, H. & Kong, L. 2014. The effect of chemical cues on the settlement of sea cucumber (*Apostichopus japonicus*) larvae. *Journal of Ocean University of China* **13**, 321–330.
- Sutherby, J., Giardini, J., Nguyen, J., Wessel, G., Leguia, M. & Heyland, A. 2012. Histamine is a modulator of metamorphic competence in *Strongylocentrotus purpuratus* (Echinodermata: Echinoidea). *BMC Developmental Biology* **12**, 14.
- Swanson, R.L., Byrne, M., Prowse, T.A.A., Mos, B., Dworjany, S.A. & Steinberg, P.D. 2012. Dissolved histamine: A potential habitat marker promoting settlement and metamorphosis in sea urchin larvae. *Marine Biology* **159**, 915–925.
- Swanson, R.L., de Nys, R., Huggett, M.J., Green, J.K. & Steinberg, P.D. 2006. In situ quantification of a natural settlement cue and recruitment of the Australian sea urchin *Holopneustes purpurascens*. *Marine Ecology Progress Series* **314**, 1–14.
- Swanson, R.L., Williamson, J.E., de Nys, R., Kumar, N., Bucknall, M.P. & Steinberg, P.D. 2004. Induction of settlement of larvae of the sea urchin *Holopneustes purpurascens* by histamine from a host alga. *The Biological Bulletin* **206**, 161–172.
- Takahashi, Y., Itoh, K., Ishii, M., Suzuki, M. & Itabashi, Y. 2002. Induction of larval settlement and metamorphosis of the sea urchin *Strongylocentrotus intermedius* by glycolipids from the green alga *Ulva lens*. *Marine Biology* **140**, 763–771.
- Takeda, S. 2008. Mechanism maintaining dense beds of the sand dollar *Scaphechinus mirabilis* in northern Japan. *Journal of Experimental Marine Biology and Ecology* **363**, 21–27.
- Taniguchi, K., Kurata, K., Manuzoi, T. & Suzuki, M. 1994. Dibromomethane, a chemical inducer of larval settlement and metamorphosis of the sea urchin *Strongylocentrotus nudus*. *Fisheries Science* **60**, 795–796.
- Tebben, J., Motti, C.A., Siboni, N., Tapiolas, D.M., Negri, A.P., Schupp, P.J., ... Harder, T. 2015. Chemical mediation of coral larval settlement by crustose coralline algae. *Scientific Reports* **5**, 10803.
- Tegner, M.J. 2001. The ecology of *Strongylocentrotus franciscanus* and *Strongylocentrotus purpuratus*. In: *Edible Sea Urchins: Biology and Ecology. Developments in Aquaculture and Fisheries Science No. 32*, J.M. Lawrence (ed.). Amsterdam: Elsevier Science, 307–331.
- Tegner, M.J. & Dayton, P.K. 1981. Population structure, recruitment and mortality of two sea urchins (*Strongylocentrotus franciscanus* and *S. purpuratus*) in a kelp forest. *Marine Ecology Progress Series* **5**, 255–268.

- Thorson, G. 1950. Reproductive and larval ecology of marine bottom invertebrates. *Biological Reviews* **25**, 1–45.
- Toha, A.H.A., Sumitro, S.B., Hakim, L., Widodo, N., Binur, R., Suhaemi, S. & Anggoro, A.W. 2017. Biology of the commercially used sea urchin *Tripneustes gratilla* (Linnaeus, 1758) (Echinoidea: Echinodermata). *Indo Pacific Journal of Ocean Life* **1**, 1–10.
- Tomas, F., Romero, J. & Turon, X. 2004. Settlement and recruitment of the sea urchin *Paracentrotus lividus* in two contrasting habitats in the Mediterranean. *Marine Ecology Progress Series* **282**, 173–184.
- Turon, X., Codina, M., Tarjuelo, I., Uriz, M.J. & Becerro, M.A. 2000. Mass recruitment of *Ophiothrix fragilis* (Ophiuroidea) on sponges: Settlement patterns and post-settlement dynamics. *Marine Ecology Progress Series* **200**, 201–212.
- Ullrich-Lüter, E.M., Dupont, S., Arboleda, E., Hausen, H. & Arnone, M.I. 2011. Unique system of photoreceptors in sea urchin tube feet. *Proceedings of the National Academy of Sciences of the United States of America* **108**, 8367–8372.
- Underwood, A.J. & Fairweather, P.G. 1989. Supply-side ecology and benthic marine assemblages. *Trends in Ecology & Evolution* **4**, 16–20.
- Uthicke, S., Doyle, J., Duggan, S., Yasuda, N. & McKinnon, A.D. 2015. Outbreak of coral-eating crown-of-thorns creates continuous cloud of larvae over 320km of the Great Barrier Reef. *Scientific Reports* **5**, 16885.
- Uthicke, S., Fisher, E.E., Patel, F., Diaz-Guijarro, B., Doyle, J.R., Messmer, V. & Pratchett, M.S. 2019. Spawning time of *Acanthaster cf. solaris* on the Great Barrier Reef inferred using qPCR quantification of embryos and larvae: Do they know it's Christmas? *Marine Biology* **166**, 133.
- Uthicke, S., Liddy, M., Patel, F., Logan, M., Johansson, C. & Lamare, M. 2018. Effects of larvae density and food concentration on crown-of-thorns starfish (*Acanthaster cf. solaris*) development in an automated flow-through system. *Scientific Reports* **8**, 642.
- Uthicke, S., Pecorino, D., Albright, R., Negri, A. P., Cantin, N., Liddy, M., Dworyanyn, S., Kanya, P., Byrne M. & Lamare, M. 2013. Impacts of ocean acidification on early life-history stages and settlement of the coral-eating sea star *Acanthaster planci*. *PLoS One* **8**, e82938.
- Uthicke, S., Schaffelke, B. & Byrne, M. 2009. A boom-bust phylum? Ecological and evolutionary consequences of density variations in echinoderms. *Ecological Monographs* **79**, 3–24.
- Valero-Garcia, A., Petrone, L., Oliveri, P., Nilsson, D.-E. & Arnone, M.I. 2016. Non-directional Photoreceptors in the Pluteus of *Strongylocentrotus purpuratus*. *Frontiers in Ecology and Evolution* **4**, 127.
- Vellutini, B.C. & Migotto, A.E. 2010. Embryonic, larval, and juvenile development of the sea biscuit *Clypeaster subdepressus* (echinodermata: Clypeasteroidea). *PLoS One* **5**, e9654.
- Vermeij, M.J.A., Debrot, A.O., van der Hal, N., Bakker, J. & Bak, R.P.M. 2010. Increased recruitment rates indicate recovering populations of the sea urchin *Diadema Antillarum* on Curaçao. *Bulletin of Marine Science* **86**, 719–725.
- Walker, J.W. 2007. Effects of fine sediments on settlement and survival of the sea urchin *Evechinus chloroticus* in northeastern New Zealand. *Marine Ecology Progress Series* **331**, 109–118.
- Walters, L.J. & Wethey, D.S. 1991. Settlement, refuges, and adult body form in colonial marine invertebrates: A field experiment. *The Biological Bulletin* **180**, 112–118.
- Wangensteen, O.S., Dupont, S., Casties, I., Turon, X. & Palacín, C. 2013. Some like it hot: Temperature and pH modulate larval development and settlement of the sea urchin *Arbacia lixula*. *Journal of Experimental Marine Biology and Ecology* **449**, 304–311.
- Warner, G.F. 1971. On the ecology of a dense bed of the brittle-star *Ophiothrix fragilis*. *Journal of the Marine Biological Association of the United Kingdom* **51**, 267–282.
- Wieczorek, S.K. & Todd, C.D. 1998. Inhibition and facilitation of settlement and epifaunal marine invertebrate larvae by microbial biofilm cues. *Biofilming* **12**, 81–118.
- Williams, S.M., García-Sais, J.R. & Yoshika, P.M. 2011. Spatial variation of *Diadema Antillarum* settlement in La Parguera, Puerto Rico. *Bulletin of Marine Science* **87**, 531–540.
- Williams, S.M., Yoshioka, P.M. & García Sais, J.R. 2010. Recruitment pattern of *Diadema antillarum* in La Parguera, Puerto Rico. *Coral Reefs* **29**, 809–812.
- Williamson, J.E., de Nys, R., Kumar, N., Carson, D.G. & Steinberg, P.D. 2000. Induction of metamorphosis in the sea urchin *Holopneustes purpurascens* by a metabolite complex from the algal host *Delisea pulchra*. *The Biological Bulletin* **198**, 332–345.
- Wilmes, J.C., Caballes, C.F., Cowan, Z.L., Hoey, A.S., Lang, B.J., Messmer, V. & Pratchett, M.S. 2018. Contributions of pre-versus post-settlement processes to fluctuating abundance of crown-of-thorns starfishes (*Acanthaster* spp.). *Marine Pollution Bulletin* **135**, 332–345.

- Wilmes, J.C., Schultz, D.J., Hoey, A.S., Messmer, V. & Pratchett, M.S. 2020. Habitat associations of settlement-stage crown-of-thorns starfish on Australia's Great Barrier Reef. *Coral Reef* **39**, 1163–1174.
- Wilson, D.P. 1978. Some observations on bipinnariae and juveniles of the starfish genus *Luidia*. *Journal of the Marine Biological Association of the United Kingdom* **58**, 467–478.
- Wing, S.R., Botsford, L.W., Largier, J.L. & Morgan, L.E. 1995a. Spatial structure of relaxation events and crab settlement in the northern California upwelling system. *Marine Ecology Progress Series* **128**, 199–211.
- Wing, S.R., Largier, J.L., Botsford, L.W. & Quinn, J.F. 1995b. Settlement and transport of benthic invertebrates in an intermittent upwelling region. *Limnology & Oceanography* **40**, 316–329.
- Yamaguchi, M. 1973. Early life histories of coral reef asteroids, with special reference to *Acanthaster planci* (L.). In: *Biology and Geology of Coral Reefs (Vol. 2: Biology)*, O.A. Jones & R. Endean (eds). New York: Academic Press, 369–387.
- Yamakawa, S., Morino, Y., Kohtsuka, H. & Wada, H. 2020. Retinoic acid signaling regulates the metamorphosis of feather stars (Crinoidea, Echinodermata): Insight into the evolution of the animal life cycle. *Biomolecules* **10**, 37.
- Yazaki, I. & Harashima, H. 1994. Induction of metamorphosis in the sea urchin, *Pseudocentrotus depressus*, using L-glutamine. *Zoological Science* **11**, 253–260.
- Yokoyama, L.Q. & Amaral, A.C.Z. 2011. Recruitment and growth variation of *Ophionereis reticulata* (Echinodermata: Ophiuroidea). *Invertebrate Reproduction & Development* **55**, 73–81.
- Yool, A.J., Grau, S.M., Hadfield, M.G., Jensen, R.A., Makell, D.A. & Morse, D.E. 1986. Excess potassium induces larval metamorphosis in four marine invertebrate species. *Biology Bulletin* **170**, 255–266.
- Young, C.M. & Chia, F.-S. 1982. Factors controlling spatial distribution of the sea cucumber *Psolus chitonoides*: Settling and post-Settling behavior. *Marine Biology* **69**, 195–205.
- Young, C.M. & Chia, F.-S. 1984. Microhabitat-associated variability in survival and growth of subtidal solitary ascidians during the first 21 days after settlement. *Marine Biology* **81**, 61–68.
- Young, C.M. & Chia, F.-S. 1987. Abundance and distribution of pelagic larvae as influenced by predation, behavior, and hydrographic factors. In *Reproduction of Marine Invertebrates Volume IX, General Aspects: Seeking Unity in Diversity*, A.C. Giese et al. (eds). Palo Alto, California: Blackwell Scientific Publications & Pacific Grove, California: Boxwood Press, 385–463.
- Yu, X., He, W., Gu, J.D., He, M.X. & Yan, Y. 2008. The effect of chemical cues on settlement of pearl oyster *Pinctada fucata martensii* (Dunker) larvae. *Aquaculture* **277**, 83–91.
- Zann, L.P., Brodie, J., Berryman, C. & Naqasima, M. 1987. Recruitment, ecology, growth and behavior of juvenile *Acanthaster planci* (L.) (Echinodermata: Asteroidea). *Bulletin of Marine Science* **41**, 561–575.