



Consequences for nekton of the nature, dynamics, and ecological functioning of tropical tidally dominated ecosystems

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ABSTRACT

The shallow waters of the world's coasts comprise a variety of ecosystems such as tidal wetlands, salt marshes, sand flats, rocky coasts, and coral reef flats, and encompass complexes of pelagic and benthic, vegetated and unvegetated habitats. These disparate ecosystems are bound together by one common feature; that the pattern of life for marine organisms, the outcomes of process and the functioning of the ecosystems are irrevocably influenced by the tide. Focusing on the tide highlights a unique component, the intertidal zone – an area that alternates between exposure to the atmosphere and inundation by marine waters. While the tide has diverse influences on the pattern of life and on the processes that regulate ecological function in *tidally dominated ecosystems*, much of this can be captured in one idea, that the multi-scale predictability of tides provides vital information for the organisms utilising these systems. We explore this idea by considering the dynamics of the nekton assemblages of *tidally dominated ecosystems*, the roles that nekton play in the functioning of those systems, and how these dynamics are fundamentally influenced by the differential responses of nekton and their prey to the predictability of tides. Further, we discuss the nature of the information tides provide to biota, the trade-offs inherent in utilising tidally available resources, and strategies employed by biota to take advantage of the tidal information and the need for strategic trade-offs.

1. Introduction

The shallow waters of the world's coasts comprise a variety of ecosystems: tidal wetlands, estuaries, salt marshes, sand flats, rocky coasts, coral reef flats and many more, encompassing complexes of pelagic and benthic, vegetated and unvegetated habitats (Litvin et al., 2018; Whitfield et al., 2022). Regardless of the specific system and characteristics, these disparate ecosystems are bound together by one common feature, that the pattern of life for marine organisms, the outcomes of processes and the functioning of the ecosystems are irrevocably influenced by the tide. Of course, the tide influences all marine environments to a greater or lesser extent, but for the purposes of this discussion, we will focus primarily on *tidally dominated ecosystems* comprising coastal waters less

than about 3 m deep at low tide. Often there are substantial changes in species composition below this depth that are consistent across habitat types (Bradley et al., 2019).

Each of these shallow coastal ecosystems comprises a mosaic of habitats that interact within the day-to-day lives of organisms (Rozas, 1995; Sheaves, 2009; Nagelkerken et al., 2015). It is the joint values of these integrated components that support ecological function. Indeed, despite the common focus of research on visually dominant components such as mangroves, in the tropics (Sheaves et al., 2020), many other components of this mosaic have substantial, often underappreciated, values (e.g., unvegetated coastal flats: Lee, 2004; Kwon et al., 2020; Chen and Lee, 2022; Crook et al., 2022).

Each mosaic component is used by a variety of taxonomically and

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trophically disparate organisms. Although these components are functionally intertwined not all organisms use the same set of mosaic components to the same extent or in the same way (Sheaves, 1996). At a larger spatio-conceptual scale, organisms move through and connect *shallow coastal ecosystems* to other marine and terrestrial ecosystems, meaning shallow coastal ecosystems operate as components of a larger meta-ecosystem; a series of spatially coupled ecosystems bound together by fluxes of energy, matter and organisms (Loreau et al., 2003).

The functioning of these shallow coastal ecosystems is much more complex than local source-sink dynamics, and features complex and diverse fluxes operating over multiple scales and in diverse directions. The components of this complex of shallow coastal ecosystems include a diversity of ecosystems with contrasting natures and structural complexity (e.g. intertidal sand flats vs rocky shores), as well as ‘similar’ ecosystems occurring in different settings (e.g. unvegetated sandflat ecosystems within estuaries and apparently equivalent unvegetated sandflat ecosystems situated along coasts), with these differences influencing the details of functional outcomes (Rozas, 1995; Bradley et al., 2020).

A focus on the tide highlights a unique component, the intertidal zone – an area that alternates between exposure to the atmosphere and inundation by marine waters. The idea that the intertidal is simply an additive habitat, providing additional resources for terrestrial or subtidal marine organisms, has been superseded by the understanding that intertidal areas are critical to the processes that affect the productivity of coastal ecosystems (Rozas and Minello, 1998; Kwon et al., 2020; Chen and Lee, 2022). While the tide has diverse influences on the pattern of life and on the processes that regulate ecological function (i.e., the movement and storage of energy or material (Bellwood et al., 2019)) in *tidally dominated ecosystems*, much of this can be captured in one idea; that the multi-scale predictability of tides provides vital *information*

(O'Connor et al., 2019) that organisms employ to optimise their spatio-temporal utilisation of the various components of the habitat mosaics available to them, resulting in complex, but predictable, ecological outcomes (Sheaves, 2009; Nagelkerken et al., 2015; Reis-Filho et al., 2016; Litvin et al., 2018). To explore this idea, we focus on nekton, as mobile mid- to upper-level consumers that utilise intertidal areas and are extensively engaged in cross-boundary connectivity and nutrient/energy translocation (Nagelkerken, 2009; Pittman, 2017). We consider how the dynamics of the nekton that make extensive use of intertidal areas of *tidally dominated ecosystems*, and the roles they play in the functioning of those systems, are fundamentally influenced by the differential responses of nekton and their prey to the predictability of tides.

2. Tides, tidal predictability & tidal information

Tides differ from place to place, varying in daily, spring/neap and annual patterns, the number of tides per day, tidal range, and the timing and duration of inundation of intertidal areas (Fig. 1). Although the exact tidal pattern can be modified by factors such as bathymetry (Terker et al., 2014), barometric pressure (Crinall and Hindell, 2004), and the influence of meteorological systems (Rozas, 1995; El-Geziry, 2013; Chiu and Small, 2016), by their nature tidal patterns are substantially predictable for any particular location. Even in microtidal systems, where meteorological events can frequently distort or even override predicted tidal patterns, the underlying tidal rhythms still dominate life in these shallow coastal systems (Rozas, 1995). Moreover, regardless of the pattern of tides, the repeated regular inundation and exposure of intertidal habitats means that the biota of coastal ecosystems interact with a mosaic of habitats that features predictably changing physical conditions (moisture, depth, temperature, dissolved

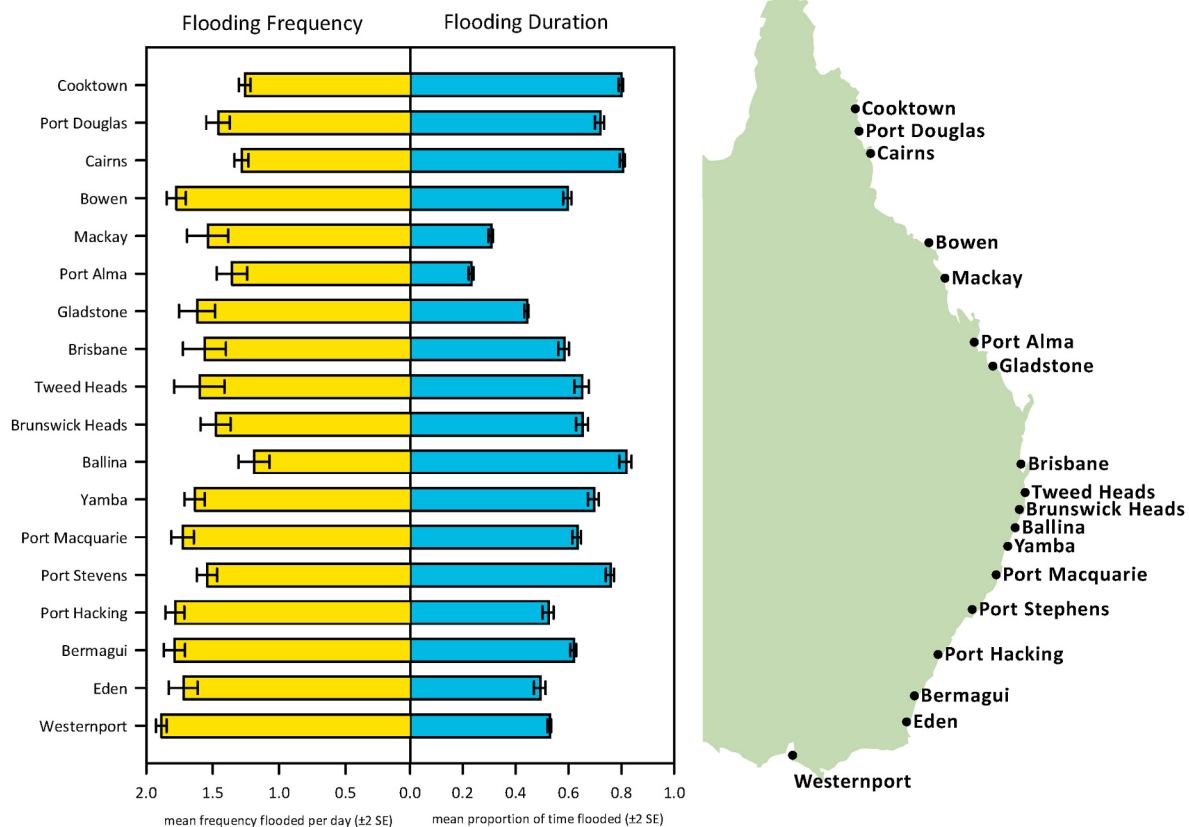


Fig. 1. Tidal flooding and duration of the seaward edge of vegetated wetlands along the east coast of Australia. Data are calculated from seasonal data for years 2005–2010. All sites had valid data for at least 20% of seasons in that period. Detailed methods can be found in Baker et al. (2015).

oxygen etc.). This tidal rise and fall cues the activities of sedentary biota (Bos et al., 2011) and regular movements of mobile biota (Frias-Torres et al., 2007; Unsworth et al., 2007; Sheaves, 2009; Nagelkerken et al., 2015). For many of these organisms, the motivation of these regular movements is the need to utilise an inundation driven, temporal chain of habitats in order to furnish life-supporting needs (Rozas, 1995; Dor-enbosch et al., 2004). The extent, regularity and duration of utilisation of intertidal areas varies with tidal pattern and range (Krumme, 2009; Baker et al., 2015). Indeed, in microtidal areas with strong meteorological influences, such as US Gulf Coast, the effects of the tide may be overridden for long periods by meteorological factors (Smith, 1979; Rozas, 1995). However, even in microtidal areas access to intertidal areas remains important (Rützler and Feller, 1988; Rozas and Minello, 1998; Dubuc et al., 2019b). Consequently, the predictable rise and fall of the tide provides vital information that coastal marine organisms constantly utilise in conducting their day-to-day lives. As a result, the lives of organisms and the functions to which they contribute, are defined to a substantial extent by the information contained in patterns of flooding/exposure.

The information provided by tidal flooding/exposure is context-independent, from the point of view that the same information (the extent, duration and timing of flooding/exposure) is available to organisms utilising a particular tidal level anywhere. However, the

outcomes for any particular situation are modified by a variety of context-dependent factors. For instance, the ability of organisms to utilise particular areas and particular intertidal levels, and the resources available there (Krumme et al., 2008), will be governed by the interaction of the tide and a range of contextual factors, (climate, chemo-physical, geological, geomorphological, biological etc.). A striking example is the fundamental difference in the nature of different types of upper intertidal areas (saltmarsh vs mangrove vs intertidal freshwater swamp forest vs saltpan (e.g. Liu et al., 2017)) as a result of differential interplay of climates and tides. This interaction of structuring forces means that outcomes for different organisms, communities and functional groups, are differentiated by their particular responses to the specific suite of context-dependent and context-independent factors that primarily influence them (Litvin et al., 2018). Together, the accumulation of these differences determines functional outcomes in terms of flows of Energy, Matter, Organisms and Information, within and between components of tidally dominated ecosystems.

Despite the fact that there are multiple forces at play, it is the tide that stimulates predictable responses within the constraints of environmental variability, and so provides a starting point for understanding the ecology and function of intertidal areas, and their role in supporting the functioning of marine ecosystems in general. The idea that tidal flooding/exposure has a fundamental influence on the nature of the

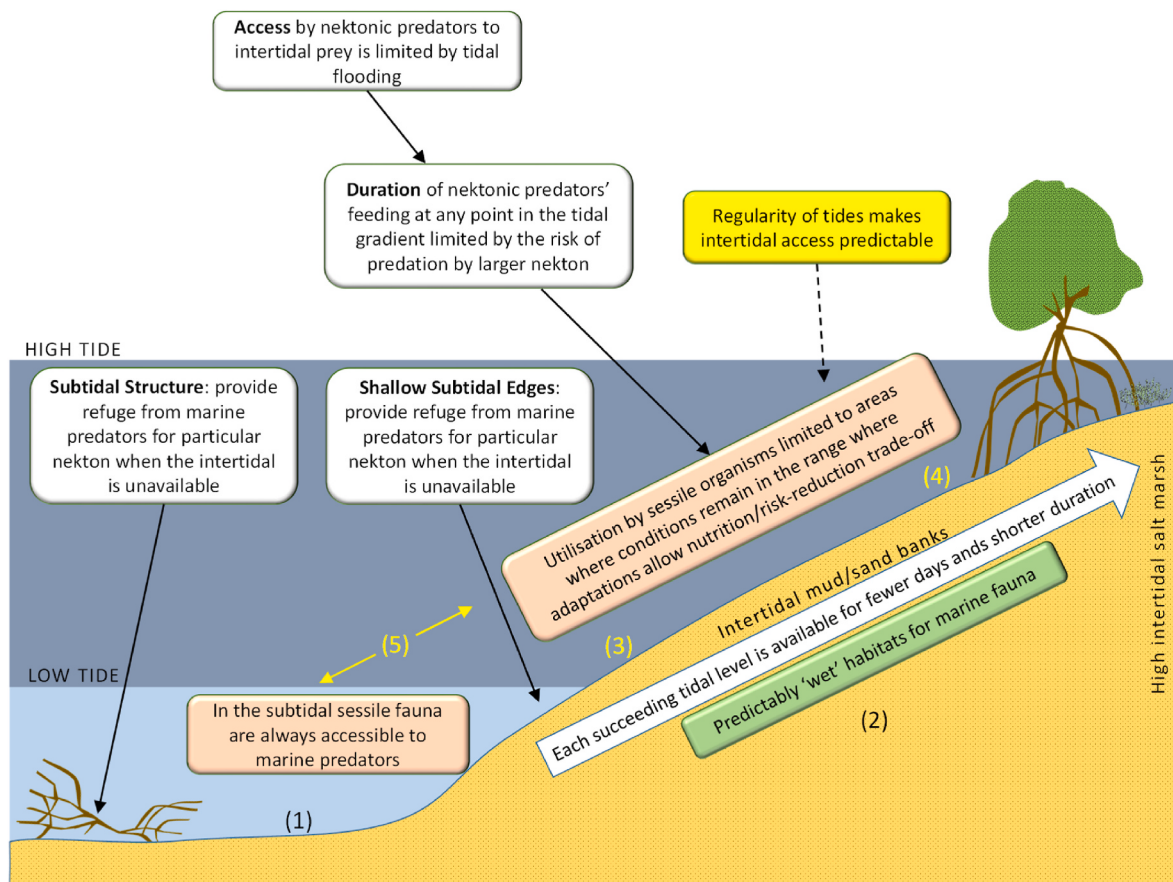


Fig. 2. Challenges and solutions in shallow tidal waters: (1) Subtidal areas are always available to marine predators providing a constantly high-risk habitat for attached- and in-fauna that lack appropriate defensive structures or behaviours. (2) Intertidal areas provide predictably 'wet' habitats suitable for occupancy by many marine fauna. Predatory nekton are excluded at low tide, but intertidal habitats become available to predatory birds, and vice versa at high tide. (3) Low intertidal areas are flooded every day, and remain continually flooded when tidal ranges are not extreme, particularly during neap tides. The regular availability of access to marine predators means that the risk of predation is high but, at the same time, low-intertidal areas provide suitable conditions for site-attached fauna with a requirement for almost continual moisture. (4) Mid/Upper intertidal habitats are not flooded every day, so conditions are less favourable for many site-attached marine fauna. However, the balance between regular wetting and regular periodic exclusion of mobile predators means that the diversity and abundance of site-attached fauna often peaks there. (5) The situation is different for mobile fauna, with the shallowest parts of the subtidal providing refuge from marine predators when intertidal areas are exposed to the atmosphere, and affording staging areas from which they can progress across the intertidal zone as water levels rise. (Similar, arguments exist relating to access to the intertidal by terrestrial/avian predators, with the logic generally working in reverse).

ecology of shallow water *tidally dominated ecosystems*, has important implications for the values of different intertidal habitats to coastal/estuarine biota, the roles that various intertidal habitats play in the ecology of systems, and the nature and consequences of inter-habitat connectivity.

3. Food/predation trade-off as a key driver of pattern and process in the lives of nekton in tidally dominated ecosystems

A trade-off between two forces shapes the everyday lives of biota – the need to acquire nutrition while minimising the risk of damage or mortality (Gilliam and Fraser, 1987; Burrows, 1994; Kneib and Wagner, 1994). This is an asymmetric trade-off, where the success of any individual feeding event is not vital but preventing mortality or serious injury is a necessity. This trade-off is particularly exigent for organisms that use intertidal areas of *tidally dominated ecosystems* because the different tidal levels offer a variety of environments and a variety of challenges for marine benthic infauna, their prey, and their predators (Fig. 2). In turn, the substantial changes in the environments over the course of the tidal cycle brings the consequent need to either migrate among habitats or possess behavioural (e.g., burrowing) (Bellwood, 2002), structural (e.g., hard external cuticle) (Whitear and Mittal, 1984) or physiological (e.g., atmospheric respiration) (Lee et al., 2005) adaptations to deal with the tidally-induced changes to physical stressors, mortality risk and food availability. Consequently, site-attached/sessile organisms are limited to areas where conditions remain within the range where their adaptations are effective at allowing the nutrition/mortality risk-reduction trade-off (e.g., Johnson and Smee, 2014). In contrast, access by mobile species is limited by tidal flooding, with the duration of access further restricted by the increased risk of predation by larger nekton as water depths increase. Therefore, both site-attached and mobile organisms face a complex set of challenges in terms of their ability to survive and thrive within their respective habitats (Davis et al., 2017).

The sequential scaling up and down of feeding opportunities, and location-specific predation risk that are cued by the tide, together with the constraints of optimal foraging and maintaining physiological homeostasis (Dubuc et al., 2019a; Kroeker et al., 2021), mean that for any species optimal food acquisition/activity will usually be confined to a small temporal window. This is equally the case for a site-attached invertebrate that requires damp sediment for efficient feeding (Cameron, 1966), but is exposed to predatory nekton when sand flats are flooded by the tide (Webb and Eyre, 2004), for a specialist predatory fish that utilises ambush positions on shallow water margins as the tide floods (Baker and Sheaves, 2006), for predators that move in with the tide to feed on juvenile nekton (Ellis and Gibson, 1995; Roemer et al., 2016), and even for predatory wading birds that target nekton moving onto shallow flats when water levels favour hunting (Dorfman et al., 2001). In each case the information in regular tidal changes provides the cue for the initiation and duration of the activities of different species, resulting in a predictable temporal sequence, with different species undertaking specific activities during windows of time when conditions are optimal for those activities. This leads to activities that are tidally predictable within specific contextual situations (Bradley et al., 2020).

The lives of site-attached organisms (e.g., invertebrate in- and epifauna) are attuned to particular tidal levels, where most remain throughout their adult lives. In contrast, for nekton, life in *tidally dominated ecosystems* poses challenges that vary with their prey acquisition and mortality avoidance strategies. Most nekton that utilise intertidal areas must migrate between tidal levels in concert with the rise and fall of the tide. There are exceptions of course; portunid crabs that can bury in wet sediment (Bellwood, 2002) and mudskippers that have taken on a sedentary semi-terrestrial lifestyle (Bennett et al., 2018). While many nekton may have utilisation strategies not tied explicitly to the use of intertidal areas, their occupation of tidally dominated areas still requires them to respond to changing tidal levels (Kneib and

Wagner, 1994; Pittman and McAlpine, 2003). Not only does the rising tide provide the opportunity to range over much greater areas, their feeding and refuge requirements mean they need to respond to the opportunities and risks presented by the spatio-temporal movements of other organisms (Dorenbosch et al., 2004).

The food acquisition/predation risk-reduction trade-off plays out differently for different species depending on their needs and adaptations. Indeed, the ways that organisms interact with these systems are complex and nuanced, and can be conceptualised as a series of hierarchy of levels (Fig. 3). At the highest level is the pattern of *Occupancy* of Coastal Systems (Fig. 3a), with a contrast between *Residents* that remain in coastal systems throughout their lives and *Transients* that make use of coastal systems for only part of their life cycles (Bretsch and Allen, 2006). Within those patterns of occupancy lie *Temporal Patterns* of intertidal utilisation (Fig. 3b), with some nekton being essentially *Permanent Inhabitants* able to remain in intertidal areas throughout the tide, others *Tidal Migrants* that move in and out of the intertidal in concert with the tides, and still others *Rare/Incidental* users of intertidal areas. *Tidal migrants* show two patterns of utilisation (Fig. 3c), *Strategic* utilisation by nekton that access intertidal areas principally to make use of resources only available there, and *Roving* utilisation by nekton that access intertidal areas as an incidental part of the movements to feed on mobile prey (Wirjoatmodjo and Pitcher, 1984). Utilisation by *Permanent Inhabitants* is essentially wholly *Strategic*.

4. Nekton utilisation of intertidal areas

Nekton that make only rare or incidental use of intertidal areas (Fig. 3) may still make use of tides to gain access to shallow subtidal areas at high tide, however it is the *Permanent Intertidal Inhabitants* and *Tidal Migrants* that are most intimately engaged in the pattern and process of life in intertidal areas, and so most extensively engaged in ecological functioning.

4.1. Permanent intertidal inhabitants

Permanent intertidal inhabitants include gobies that remain in intertidal areas at low tide by utilising pools formed in stingray pits (Chargulaf et al., 2011), blennies and gobies that inhabit intertidal rockpools (Arakaki and Tokeshi, 2006; Faria and Almada, 2006), mudskippers that utilise physiological and behavioural adaptations (Lee et al., 2005) to remain in mangroves throughout the tide (Bennett et al., 2018), fundulids and cyprinodontids that are specialised to occupy small depressions, fossorial niches, or shallow wetland pools despite extremes in temperature and DO (Taylor, 2000; Smith and Able, 2003), and portunid crabs that possess suites of adaptation that allow them to remain buried in soft sediments during low tide (Vezzosi et al., 1994; Bellwood, 2002). In fact, as a result of impressive adaptations to harsh and variable physical and chemical conditions in intertidal areas, species such as gobies, blennies and mudskippers often dominate fish numbers on the intertidal flats or mangrove forests in which they are found (Arakaki and Tokeshi, 2006; Chargulaf et al., 2011; Bennett et al., 2018). *Transient* species with appropriate adaptations may take up *Permanent* intertidal habitation during their residence in coastal ecosystems, however *Permanent inhabitants* mainly comprise *Resident* species, although even for those, utilisation of intertidal areas may be life-cycle stage dependent (Hill et al., 1982).

4.2. Tidal migrants

Tidal Migrant nekton include both *Transient* and *Resident* nekton that lack adaptations (e.g., abilities to survive depressed dissolved oxygen levels (Dubuc et al., 2021)) tolerance for permanent occupation of intertidal areas. As a result, they move from permanently submerged subtidal areas to intertidal areas, in concert with the rise and fall of the tide to access the resources available there. They display many nuanced

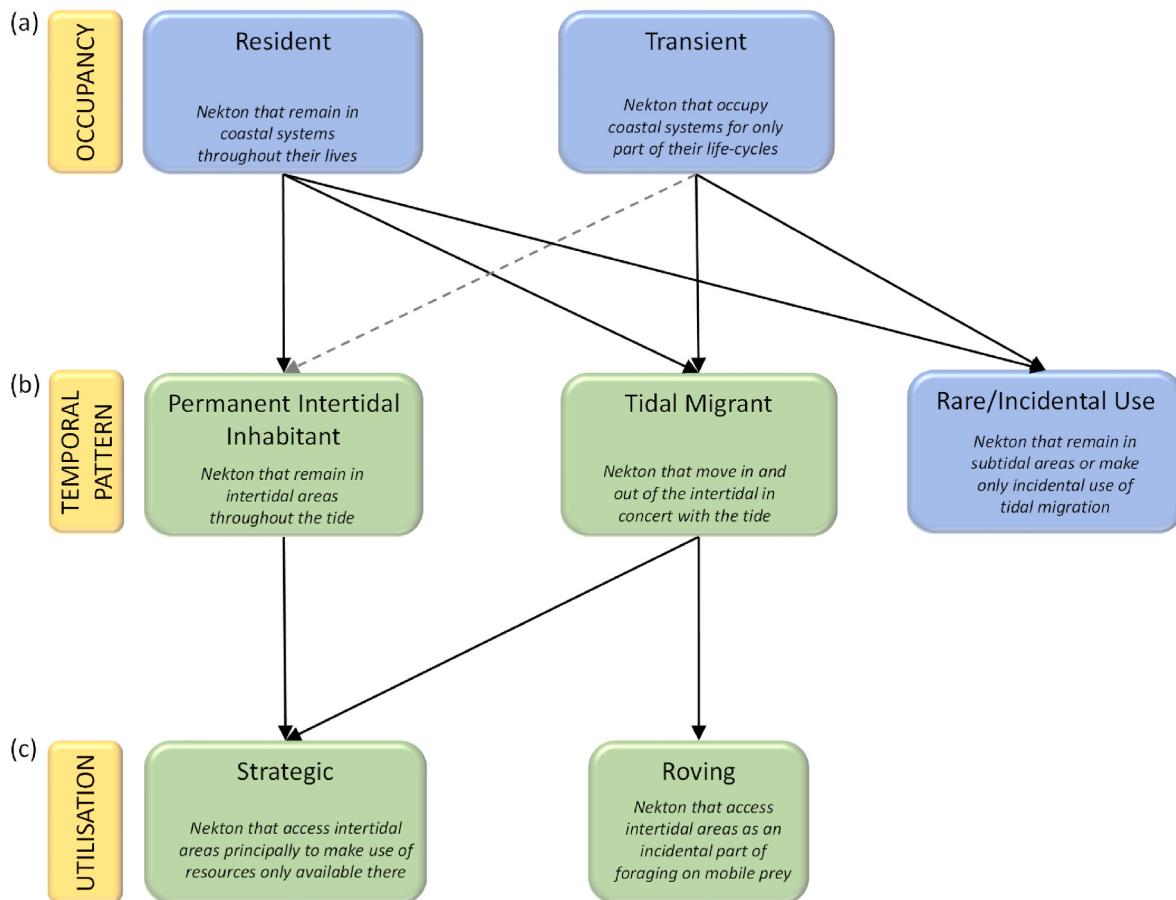


Fig. 3. Levels of organismic interaction with tidally dominated ecosystems. At the highest level is (a) the pattern of occupancy, within that are (b) various temporal patterns of use, again nuanced by (c) a variety of patterns of utilisation. The components relevant to intertidal utilisation are indicated by green boxes and their relationships by arrows. The dashed arrow indicates that ‘Transient Occupants’ are only ‘Permanent Intertidal Inhabitants’ for part of their life-histories. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

patterns of tidal movement (Fig. 4). There are two broad categories of *Tidal Migrant* nekton that utilise intermittently flooded intertidal areas: *Strategic migrants* that access intertidal areas principally to make use of resources only available there, and *Roving* species that access intertidal areas as an incidental part of foraging on mobile prey.

Strategic Migrants: Species that utilise a *Strategic Migration* strategy are most obviously dependent on the tides. These nekton migrate with the tide to access intertidal food sources (Sheaves and Molony, 2000; Zagars et al., 2012; Roemer et al., 2016; Sheaves et al., 2016b; Dubuc et al., 2019b). Many strategic migrants use these regular migrations to remain in water shallow enough to limit the risk of predation by most predatory nekton (Burrows et al., 1994; Dorenbosch et al., 2004). Although these species utilise a common tidal migration strategy, they comprise species with diverse trophic identities that range from benthic invertebrate feeders, through specialised and opportunistic predators, to herbivores and phytodetritivores (Davis et al., 2014).

Benthic invertebrate feeders include taxa such as whiting (Sillaginidae) (Gray et al., 1998; Krück et al., 2009) and stingrays (Dasyatidae) that follow the tide to access rich intertidal benthic prey resources (Crook et al., 2022), and lutjanids specialising on feeding in mangrove forests (Sheaves and Molony, 2000; Zagars et al., 2012). Shallow-water specialist predators include platycephalids that position themselves in shallow water to ambush invertebrate-feeding nekton as they move to take advantage of the feed opportunities afforded by the rising tide (Baker and Sheaves, 2006). Opportunistic predators include a diversity of taxa such as hammerhead sharks (e.g., *Sphyrna mokarran*) that move into shallow waters to feed on juvenile stingrays and fish (Roemer et al., 2016), and barracuda (Sphyraenidae) that take up advantageous

positions from which to employ a lie-in-wait strategy to attack passing prey with and explosive rush (Hiatt and Strasburg, 1960; Porter and Motta, 2004; Gerking, 2014). Browsing herbivores include Rabbitfish (Siganidae) that access intertidal seagrass beds (Moussa, 2018; Espadero et al., 2020), while phytodetritivores such as mugilids feed on unvegetated flats (Abrantes and Sheaves, 2009; Lee et al., 2019a).

Patterns of tidal migration may be complicated by diurnal/nocturnal migrations undertaken to take advantage of day/night differences in predation risk and/or prey availability. As a result, patterns of tidal migration may differ between day and night (Burrows et al., 1994), with the relative importance of tidal diurnal/nocturnal components being location- and context-specific (Burrows, 1994). The result of this complexity is that, as well as utilising the different resources made available by the tide in a variety of ways, nekton utilising this strategy influence the functional outcomes of cross-boundary connectivity, in terms of energy and matter transfer, storage and mobilisation.

Food resources are not spatio-temporally homogeneous, rather different prey aggregate at different tidal levels (Burrows, 1994; Dittmann, 2000; Sheaves et al., 2016a), with the various intertidal prey resources each taxon targets accessed predictably on a quasi-daily basis depending on the tide (Burrows, 1994; Baker et al., 2015). Specific predators specialise on targeting prey at particular tidal levels (Minello et al., 1991; Rozas and Minello, 1998). For instance, in the same systems whiting (*Sillago* spp.) (Hargreaves et al., 2017) and stingrays (Crook et al., 2022) feed on infauna occupying lower intertidal flats, while mangrove red snapper, *Lutjanus argentimaculatus* specialises on mangrove-dependent crabs (Sheaves and Molony, 2000).

Regular forays into specific intertidal areas requires complex

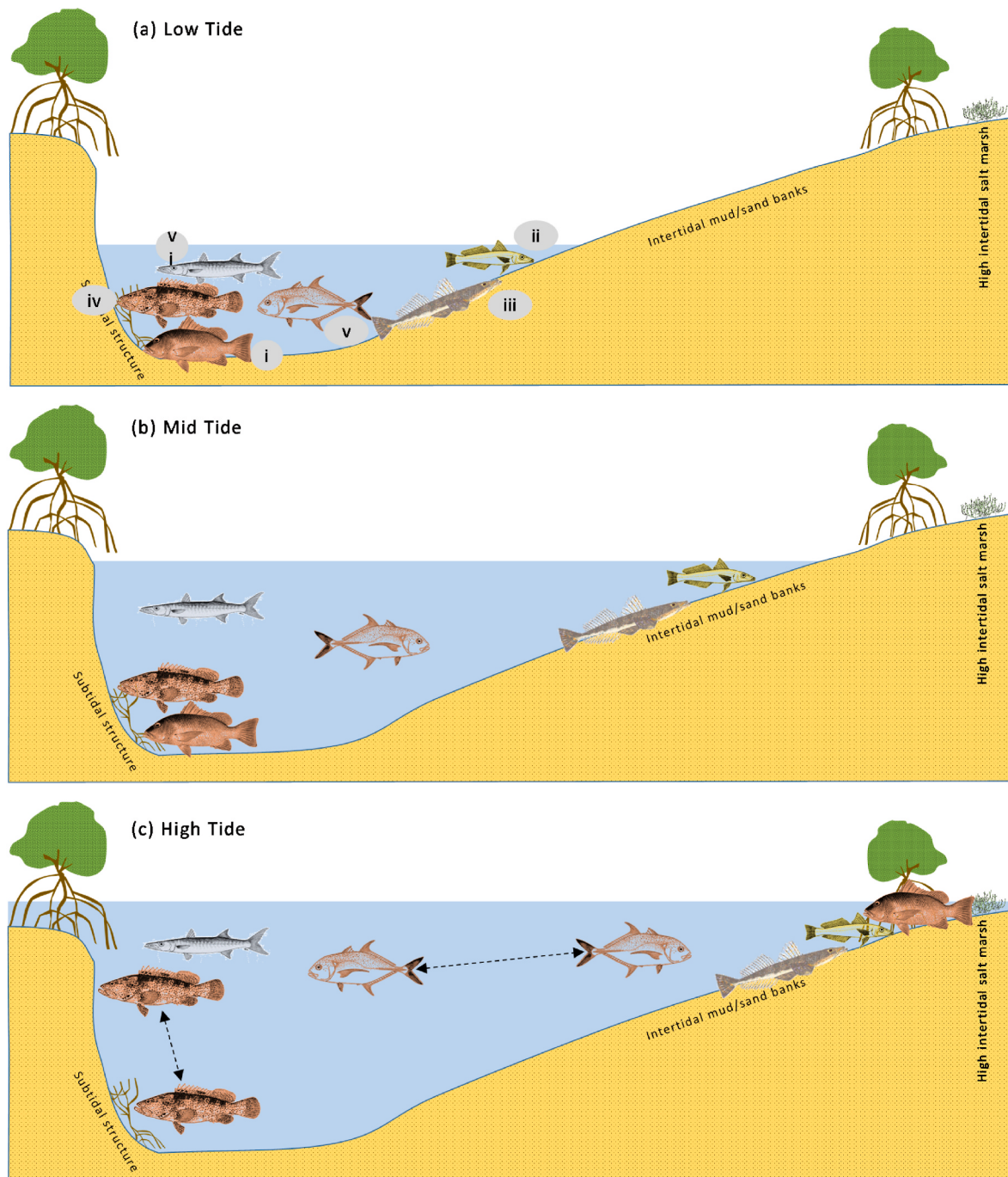


Fig. 4. Some tidally referenced spatial distribution patterns based on 5 representative species from Australian tropical estuaries: (i) The mangrove specialist *Lutjanus argentimaculatus* that makes tidal migrations between low tide refuge structures once the mangrove forest is tidally inundated, (ii) The shallow water migrater *Sillago ciliata*, that migrates with the tide to feed on intertidal benthos, remaining in water shallow enough to limit risk from most predatory nekton throughout the tide, (iii) The specialist intertidal predator *Platycephalus fuscus* that migrates with the tide, burying in shallow water to ambush other migrating fish, (iv) The structure associated *Ephinephelus malabaricus* that remains associated with complex bankside structure throughout the tide, but may migrate vertically to access prey such as mangrove crabs, (v) the cursorial predator *Caranx papuensis* that roves in search of prey aggregations and targets predictable 'hot spots' (e.g. the mangrove edge as the falling tide forces nekton to move from cover), and (vi) the lie-in-wait predator *Sphyrna putnamae* that takes up an advantageous position and attacks prey with a sudden lunge when they approach in range, often migrating vertically to remain in near-surface waters. Arrows in (c) indicate species with variable locations over the tide, *C. papuensis* with a roving strategy and *E. malabaricus* that may migrate higher on steep mud banks as the tide rises to access prey.

management of the consequent predation risks (Hammerschlag et al., 2010). Remaining in shallow water habitats throughout the tide reduces the risk of predation from many, but not all, predatory nekton (e.g. shallow water specialist piscivores (Baker and Sheaves, 2006)). At the same time, it heightens the risk of avian predation and often involves the utilisation of predation risk reducing strategies/adaptations, such as

burying or aggregating behaviours, highly tuned flight responses, countershading or the possession of toxins (Fuiman and Magurran, 1994; Crowder et al., 1997; Ryer et al., 2004). Feeding in intertidal habitats requires strategic responses to limit predation risks during low tide, non-feeding periods (Sheaves, 2009). For some species this can be achieved by remaining in shallow habitats at low tide (Crowder et al.,

1997), while other species move to structurally complex low tide refuges (Johnston and Sheaves, 2007; Sheaves, 2009; Davis et al., 2017). Regardless of the strategy, as long as prey remain abundant at a location, it is more beneficial for *Strategic Tidal Migrants* to remain close to the predictable feeding area than to expend energy moving around a system increasing exposure to predation risk.

Roving Nekton: Mobile prey are not distributed regularly nor even randomly through subtidal waters, but rather occur as spatially dispersed and temporally intermittent aggregations (Fauchald, 1999; Omundsen et al., 2000). These aggregations result from tidal migrations, which reduce predation risk by allowing vulnerable nekton to remain in shallow waters (Rypel et al., 2007) or to access complex structures made available by the flooding tide and/or to access time and tide-specific prey resources (Sheaves et al., 2016b). These tidal migrations result in constant spatio-temporal variability in prey location, abundance and availability, that requires their predators to employ a *Roving Strategy* to find and access prey aggregations across both subtidal and intertidal areas.

Depending on species, nekton utilising a *Roving* prey acquisition strategy forage within small or large areas to detect spatially dispersed and temporally intermittent prey aggregations, or to feed on prey that become temporarily vulnerable (Fauchald, 1999). A roving strategy typically involves periods of searching and times of occupancy of specific areas, either because these are areas of predictable prey encounter or non-feeding resting areas (Fauchald, 1999). Specific patterns of activity vary greatly within a roving strategy. Schooling piscivores such as carangids, and planktivores such as clupeids rove over substantial areas in search of prey, often moving among sites of potential prey aggregation. In contrast, estuarine sparids with broad diets (Sheaves, 1993) undertake more local movements, taking advantage of whatever local prey resources are available (Sheaves et al., 2014b).

Although *Roving strategists* need not be tightly bound to intertidal utilisation, tides still play a critical role in their lives. Tidal information enables them to access sites at times when prey aggregations occur predictably within their occupied niche – in effect reducing uncertainty in prey encounter. For instance, in meso- and macro-tidal estuaries the substantial changes in volume and connectivity produced by the tide can determine the location and timing of prey aggregations (Morgan et al., 2005). In addition, changes in depth and tidally-induced currents produce prey aggregation ‘hot spots’, in areas such as the mouths of estuaries, or plume fronts (Swieca et al., 2020) that provide particularly favourable sites for the aggregation of prey, or places in time where prey are forced to move between tidally available refuge areas, placing them at heightened risk of predation (Sheaves, 2005; Hammerschlag et al., 2010). A *roving strategy* enables nekton to move among hot spots of prey aggregation taking advantages of feeding opportunities as they change over time.

5. Consequences of nekton utilisation of intertidal areas

The need for nekton to respond to the information provided by the tide, and to move between components of the mosaic of habitats that comprise *tidally dominated ecosystems* (Sheaves, 2009), shapes the patterns of their lives and profoundly influences ecosystem function. The predictability of tidal flooding and drying allows organisms to optimise their spatio-temporal utilisation of the various components of habitat mosaics to manage the trade-off between predation avoidance and efficient food acquisition. At the same time, nekton play vital roles in the function of *tidally dominated ecosystems* (Litvin et al., 2018), with functional outcomes fundamentally influenced by the differential responses of nekton and their prey to the predictability of tides.

Ecological outcomes are complex but largely predictable in *tidally dominated ecosystems*, with the tide and the responses of biota interacting to produce critical outcomes, such as mediating the translocation of productivity within and among ecosystems, and providing substantial nursery ground value. The translocations of energy, matter and

organisms (Nelson et al., 2013; Litvin et al., 2018) that are involved are dependent on the complex interlinking of physical and biological processes, meaning that the value of tidally dominated coastal ecosystems is much more than the sum of the many values attributed to component habitats such as mangroves, seagrass, saltmarsh, oyster reefs and unvegetated tidal flats (Sheaves et al., 2015).

Upload and Translocation of Energy: Marine coastal ecosystems contribute substantial quantities of carbon and nutrients to near- and off-shore waters (Eyre and McKee, 2002; Hyndes et al., 2014; Herrmann et al., 2015) both by serving as conduits for terrestrial productivity (Caddy and Bakun, 1994; Abrantes and Sheaves, 2008) and via substantial intertidal and shallow subtidal benthic and planktonic productivity (Leguerrier et al., 2003; Lee et al., 2019a; Kwon et al., 2020; Baker et al., 2021). In fact, shallow water biological processes are crucially important, with biologically mediated organic carbon fluxes often dominating physical transport fluxes (Kemp et al., 1997; Bouillon and Connolly, 2009).

Organismic activities in *tidally dominated ecosystems* contribute to the upload of coastal and terrestrial productivity into marine food webs both locally, via food web interactions (Meziane and Tsuchiya, 2000; Leguerrier et al., 2003) and tidal migrations (Krumme, 2009), and over distance across diverse offshore habitats via the migration of transient nekton (Nelson et al., 2013; Sheaves et al., 2023). The significance of engagement by nekton in intertidal food webs is manifested in the substantial biomasses of nektonic detritivores (Halliday and Young, 1996; Laffaille et al., 2000) and benthivores feeding there (Burrows, 1994; Crook et al., 2022). Linking of productivity to distant ecosystems occurs via life-history migration (Sheaves et al., 2015) as well as nekton migration for feeding, spawning or to accommodate seasonal change (Blaber et al., 1995; Pittman and McAlpine, 2003).

Nursery Value: Tidally dominated systems around the world provide nurseries for diverse ecologically, recreationally, and commercially important nekton, with up to 80% of commercial species and their key prey dependent on coastal systems (Blaber et al., 1995; Lellis-Dibble et al., 2008; Litvin et al., 2018). In particular, across many taxa, juvenile nekton are strongly associated with intertidal areas and their productivity (Lee, 2004; Castellanos-Galindo et al., 2010). However, nursery value is rarely conferred by a single habitat with intertidal areas comprising just one component of the mosaic of habitats that support nursery value (Nagelkerken et al., 2015; Litvin et al., 2018). Moreover, the nursery value of a given tidal system is not stable through time and space. Rather, tidal migrations of nekton in response to the rise and fall of the tide induce substantial variability in the use of the different components of tidal systems over relatively small time and spatial scales. As a result, if a specific component of the intertidal system is temporarily unavailable, its potential value is not fulfilled (Krumme, 2009). As with the upload and translocation of productivity, the requirement for juveniles to access to multiple habitats emphasises the importance of connectivity as a key enabler of processes across *tidally dominated ecosystems* (Sheaves et al., 2007b; Sheaves, 2009). Furthermore the perception of a coastal nursery habitat, is often linked to an area that is somewhat available on a daily basis (e.g. mangrove forests). However the cyclical changes in tidal amplitudes, also allow for some areas to only be accessible during the larger monthly tides. These areas with limited connectivity could appear to have lower nursery ground value, however the intermittent connectivity, dictated by the tides, is what confirm value to the area for some juveniles, as it can assist juvenile with predator avoidance and resources, as long as the tidal connection frequency is enough to guarantee the water quality to remain within the tolerance level of the inhabiting species (Mattone et al., 2022).

A dynamic environment: Tidal fluctuations induce rapid changes in environmental conditions such as dissolved oxygen (DO), salinity, temperature and pH that can temporarily render habitats unsuitable for fish, limiting access for many species (Elliott and Quintino, 2007; Mattone and Sheaves, 2017; Dubuc et al., 2019a). However, despite their challenging nature intertidal coastal environments are utilised by many

species. Although we lack precise understanding of the costs and benefits of tidal migrations it is assumed that being able to access tidal environments even temporarily confers advantages, particularly in terms of food resources and predatory avoidance (Gibson, 2002). However, species using intertidal environments successfully must be adapted to face highly changing environmental conditions (Andrades et al., 2018), because tidal fluctuations bring with them rapid and extreme change in physical and chemical conditions, particularly desiccation, temperature, salinity, and oxygen (Dubuc et al., 2019a; Mattone et al., 2022), that can temporarily create unsuitable conditions for fish lacking appropriate adaptations (Elliott and Quintino, 2007; Mattone and Sheaves, 2017; Dubuc et al., 2019a).

The stresses imposed by the dynamic coastal environment are exacerbated by diverse anthropogenic activities that are often most intense adjacent coastal intertidal areas. These areas are exposure to threats as diverse as dredging and landscape modification (Burt, 2014; Martín-Antón et al., 2016), pollution (Shriadah, 2000; Kroon et al., 2016; Fong et al., 2020), temperature and salinity impacts from human industry (Ibrahim and Eltahir, 2019), plastic accumulation (Martin et al., 2020), coastal eutrophication (Nicastro and Bishop, 2013b), fishing activities (Pauly et al., 2002), and impaired connectivity and altered hydrology (Sheaves et al. 2010, 2014a; Loureiro et al., 2016). Additional to, and interwoven with these, are the complex effects of climate change (Sheaves et al., 2007a; Hobbs and McDonald, 2010; Colombano et al., 2021; Gilby et al., 2021). Together these present a formidable set of challenges to long-term maintenance of the values provided by the interaction between intertidal areas and their migrating nekton.

A Resilient Biota: Organisms utilising tidally dominated areas require strategies and adaptations enabling them to overcome the costs and energetic expenditure of utilising these extreme environments (Boyd et al., 2016; McArley et al., 2019; Dubuc et al., 2021). For instance, nekton specialising in accessing intertidal areas have enhanced physiological mechanisms to better respond to the development of hypoxic conditions (Dubuc et al., 2021). Intertidal macroinvertebrate assemblages can be surprisingly resilient to eutrophication (Nicastro and Bishop, 2013a). Similarly, fish such as *Elops hawaiiensis* and *Chanos chanos* can deal with salinities of over 100‰ (130 mS/cm) (Molony and Parry, 2006), amphibious stichaeoid fishes possess substantial abilities to resist desiccation (Horn and Riegler, 1981), while juvenile *Lutjanus argentimaculatus* occupy estuarine waters spanning fresh to hypersaline salinities (Mattone et al., 2022) and are tolerant to very depressed dissolved oxygen (DO) levels (Dubuc et al., 2019a; Mattone et al., 2022). These strategies appear to be the result of phenotypic plasticity favoured by the exposure to fluctuating environmental conditions or evolutionary adaptations (Kelly et al., 2016; Kroeker et al., 2020) resulting in higher adaptive potential, however, understanding of the mechanisms underpinning species' resilience to environmental extremes is incomplete.

Because environmental factors can change rapidly and simultaneously in tidally dominated ecosystems, organisms need to be able to respond quickly either by avoiding harmful areas to maintain physiological homeostasis, or by resorting to physiological adjustments over the relevant time frames (Martin, 1995; Kroeker et al., 2020; Blewett et al., 2022). Consequently, they rely on information from endogenous or exogenous factors to determine when to be active, when and where to migrate to maximise the benefits and minimise risk (Gibson, 2002). This information can come from many sources. For instance, in order to prevent stranding, many fish use changes in hydrostatic pressure to inform them of the rise and fall of the tide (Northcott et al., 1991), while others can track optimal temperature and dissolved oxygen levels using as cues for tidal migrations (Schurmann et al., 1998; Wannamaker and Rice, 2000).

This resilience is contingent because there are physiological limits on the extent to which organisms can adjust to a stressful environment before negative consequences on their health and fitness ensue. For instance, the resistance of macroinvertebrate assemblage to

eutrophication varies substantially among habitat types (Nicastro and Bishop, 2013a), while the use of upstream estuarine areas by juvenile fish with similar abilities to withstand low DO varies due to different salinity tolerances (Mattone et al., 2022). Consequently, many species making use of these habitats may already be living on the edge of their physiological tolerances, with any further degradation likely to have severe consequences on these dynamic systems (Dubuc et al., 2021). Consequently, despite the resilience of intertidal nekton to physical extremes, they are at considerable risk from the cumulative effects and often multifaceted impactors that stem from anthropogenic stressors and their interaction with climate change (Burt, 2014), particularly because these cumulative impacts remain poorly understood (Ben-Hasan and Christensen, 2019).

Management: Because functional outcomes in *tidally dominated ecosystems* are determined by the complex interaction of organisms across a mosaic of interacting habitats, functionality is a system-level property. As a result, management will only be successful if it is focused at a whole-of-system level, rather than on individual habitat components. The weakness of habitat-by-habitat management can be seen in the inadequacy of economic evaluations to meaningfully measure the value of these systems (Sheaves et al., 2020) and the failure of many habitat restoration projects to produce meaningful and predictable outcomes (Lee et al., 2019b). Taking a functional view will require expansion of current knowledge in three specific areas.

1. **Understanding the functional role of the species:** The organisms intimately involved in *tidally dominated ecosystems* need to be understood as functional contributors, not just as individual species. In this, it is particularly important to ensure that species that play key functional roles are understood. This requires that the full range of common species are identified and that their key habitat requirements and relationship to ecosystem processes are understood (Sheaves et al., 2021). In the past, research has been unevenly focused; often on species that are easy to study (e.g. semi-terrestrial crabs), species from high profile groups (e.g. nursery ground species (Sheaves, 1998)), or a sub-set of species of commercial value (Aksnes and Browman, 2016) or species that are yellow (Bellwood et al., 2020)! This has left many important species and functional groups poorly represented both at global and local scales. Providing the most management relevant information also requires research to be more specifically targeted. For instance, juvenile fish grow rapidly in size, resulting in constantly changing refuge requirements to account for this increasing size, and the need access prey appropriate to stage/size-specific requirements (Baker & Sheaves, 2005, 2021). At the same time, they need to remain in areas within their physiologically limits. For many species these early life stages occur in shallow coastal waters where the potential impacts of anthropogenic and climate change are greatest (Lotze et al., 2006; Halpern et al., 2008). These are particularly at-risk life cycles and management requires specific information on the critical needs of the different stages in order to identify and deal with the most acute risks (Sheaves et al., 2021). Even then research needs to extend beyond occurrence, pattern, and distribution to process and function (Minello, 2017).
2. **Habitat synergies and interactions:** All habitats need to be considered, assessed, and valued from a functional standpoint. In the past, studies have been biased towards habitats of particular interest, often vegetated, habitats such as mangroves and seagrass (Bradley et al., 2017). Other habitats, such as unvegetated intertidal sands and muds, have received relatively little study in many areas, despite having a similar global extent to mangrove forests (Murray et al., 2019; Murray et al., 2022) and their apparent value to nekton (Sheaves et al., 2012). This piecemeal understanding militates against the development of a comprehensive understanding of the functioning of *tidally dominated ecosystems*, and limits the ability for precise science-based decision making.

3. Temporal and spacial connection between habitats and species: Connectivity is a key enabler of life in *tidally dominated ecosystems*, making it a critical part of systems value. As a result, management needs to extend its focus beyond spatial units to address the details and needs of appropriate connectivity.

The lack of a comprehensive understanding of *tidally dominated ecosystems* as functional entities severely limits the ability to determine the overall or relative values of these ecosystems or their habitat mosaic components. This in turn limits well-informed decision-making in relation to management interventions aimed at effective environmental outcomes such as restoration, habitat enhancement, carbon sequestration, blue engineering and environmental offsetting, and militates against the development of meaningful measure for evaluating success.

CRediT authorship contribution statement

M. Sheaves: Writing – original draft, Conceptualization. **R. Baker:** Writing – review & editing, Validation. **K. Abrantes:** Writing – review & editing. **A. Barnett:** Writing – review & editing. **M. Bradley:** Writing – review & editing. **A. Dubuc:** Writing – review & editing. **C. Mattone:** Writing – review & editing. **J. Sheaves:** Writing – review & editing. **N. Waltham:** Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

No data was used for the research described in the article.

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