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True value of estuarine and coastal nurseries for fish: incorporating complexity and dynamics

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Abstract

Coastal ecosystems, such as estuaries, salt marshes, mangroves, and seagrass meadows,

comprise some of the world's most productive and ecologically significant ecosystems.

Currently, the predominant factor considered in valuing coastal wetlands as fish habitats is

the contribution they make to offshore, adult fish stocks via ontogenetic migrations.

28   However, the true value of coastal nurseries for fish is much more extensive, involving

29   several additional, fundamentally important ecosystem processes. Overlooking these broader

30   aspects when identifying and valuing habitats risks suboptimal conservation outcomes,

31   especially given the intense competing human pressures on coastlines and the likelihood that

32   protection will have to be focussed on specific locations rather than across broad sweeps of

33   individual habitat types. We describe 10 key components of nursery habitat value grouped

34   into three types: 1) Connectivity and population dynamics (includes connectivity,

35   ontogenetic migration and seascape migration), 2) Ecological and ecophysiological factors

36   (includes ecotone effects, ecophysiological factors, food/predation trade-offs and food webs),

37   and 3) Resource dynamics (includes resource availability, ontogenetic diet shifts and

38   allochthonous inputs). By accounting for ecosystem complexities and spatial and temporal

39   variation, these additional components offer a more comprehensive account of habitat value.

40   We explicitly identify research needs and methods to support a broader assessment of nursery

41   habitat value. We also explain how, by better synthesising results from existing research,

42   some of the seemingly complex aspects of this broader view can be addressed efficiently.

43   **Keywords**: Nursery ground – Ecosystem mosaic – Coastal wetland – Estuary – Fish

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Introduction

47   Coastal wetlands comprise some of the most valuable ecosystems on the planet (van den Belt

48   2011, Elliott & Whitfield 2011), and yet are among the most threatened (Bassett et al. 2013).

49   Their position at the interface of land and sea means they occupy locations that are highly

50   prized by humans, leading to unprecedented and rapidly increasing threats from intense

51   population pressure, rapid, large-scale development, and climate change (Hughes et al. 2009,

52   Corn and Copeland 2010). This conjunction of high value and intense threats makes a

53   detailed understanding of the functioning of coastal wetlands essential if they are to be

54   managed and protected for future generations (Elliott & Kennish 2011).

55   One value that is increasingly recognised for all types of coastal wetlands, whether they are

56   estuaries, saltmarshes, mangrove forests, seagrass meadows or floodplain swamps, is their

57   role as nursery grounds for aquatic species of immense ecological, cultural and economic

58   importance (Beck et al. 2001, Mumby and Hastings 2008). This nursery value stems from the

59   provision of habitat, refuge, food, favourable physical conditions and advantageous

60   hydrodynamics (Nagelkerken et al. in press). However, the provision of these services is

61   complex. Not only do the values manifest at a variety of scales (e.g. habitat or food provided

62   at a local scale, versus physical conditions at a whole of ecosystems level) but, rather than

63   being a function of a single habitat, their values are usually conferred by a mosaic of

64   interacting habitats (Sheaves 2009, Berkström et al. 2012) and may rely on processes or

65   inputs derived from well beyond the wetlands themselves (Beger et al. 2010). Many of the

66   processes that underpin nursery function may not be a feature of a spatial habitat at all; for

67   example, reliance on the delivery of allochthonous sources of production to support food

68   webs (Connolly et al. 2005), or the temporal coincidence of recruitment and the availability

69   of suitable prey resources (Robertson and Duke 1990). Nursery function is further

70   complicated by the diversity of life-history strategies of the species occupying these systems

71   (Elliott et al. 2007, Potter et al. in press).

72   Although estuarine and coastal ecosystems have long been recognised as nurseries for fish

73   and crustaceans (Boesch and Turner 1984), it was not until the seminal work of Beck et al.

74   (2001) that the concept was formalised. However, the ideas of Beck et al. (2001) and their

75   modification by Dahlgren et al. (2006) focus on one aspect of nursery ground value; the

76 supply of juveniles from discrete spatial units of nursery habitat to adult populations. Such

77 approaches only consider contribution that can be measured in terms of the movement of

78 juvenile numbers/biomass, so do not capture the complex dynamics that support nursery

79 function. While these approaches represent a significant step forward, comprehensive nursery

80 identification and valuation requires that the complex, dynamic nature of nursery ground

81 function needs to be recognised (Able 2005, Mumby and Hastings 2008, Sheaves 2009,

82 Potter et al. in press) and consolidated into identification and valuation if nursery function is

83 to be maintained in the face of ever increasing anthropogenic pressures (Nagelkerken et al. in

84 press).

85 There are two aspects to the value of nursery grounds to fish: (1) their value in supporting

86 successful nursery ground occupation, and (2) the value to recipient populations and

87 ecosystems (Fig. 1). Most current concepts of nursery ground value (e.g. Beck et al. 2001,

88 Dahlgren et al. 2006) relate to the output of juveniles from nursery grounds that reach

89 offshore (e.g. Reis-Santos et al. 2012), but the mechanisms that drive this contribution to

90 recipient populations are incompletely understood. Recognition of the significance of the

91 processes which regulate juvenile populations within nursery habitats is nothing new (e.g.

92 Minello et al. 2003), and the need to evaluate this information in the context of entire

93 lifecycles is increasingly recognised (Huijbers et al. 2013, Baker et al. 2014, Vasconcelos et

94 al. in press). However, current approaches to the valuation of nurseries ultimately treat the

95 processes driving nursery function as a black box by simply measuring what emerges at the

96 end as emigrants to the adult populations. The resulting rankings of nursery grounds fail to

97 provide managers with information on how to protect key processes that underpin nursery

98 value and function. Furthermore, focusing management and further research on the identified

99 'important' nursery habitats is risky because the habitat units identified will rarely contain all

100 the elements that support the nursery function we aim to protect.

101 Nursery ground value is the net result of a complex of interacting factors that vary from

102 situation to situation. Some involve seascape structure and function directly (Hammerschlag

103 et al. 2010), but others extend to include complex ecological interactions and resource

104 dynamics, and often involve a complex of cross-habitat and cross-ecosystem movements.

105 This complexity needs to be considered in the context of differences in the composition of

106 fish assemblages using coastal nurseries in different parts of the world (Sheaves 2012, Potter

107 et al. in press) that is likely to result in different mixes of factors being important in different

108 regions. Understanding this complexity and the relative importance of different factors, is the

109 key to meaningful nursery identification and valuation, and is the raw material needed to

110 inform population conservation decision support systems (Beger et al. 2010). Conversely, a

111 lack of evaluation of the complexity is the recipe for superficial assessment (Harris and

112 Heathwaite 2012) that is likely to miss the most critical contributors to value. Consequently,

113 we build on earlier work to develop a framework for a more comprehensive understanding of

114 nursery ground value, by considering the range of contributions of nurseries to sustaining

115 local production, replenishing adult stocks and influencing recipient ecosystems. We also

116 consider approaches available to identify the range of factors underpinning nursery value at a

117 particular site, the extent to which they contribute to nursery value and the factors that need

118 to be taken into account to inform comprehensive, effective and well-grounded management

119 decisions. At face value, recognising and including this complexity seems a difficult task, but

120 most of the research needed to underpin this consolidation is already being conducted; it just

121 needs to be integrated and extended.

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123 **Factors Supporting Successful Nursery Ground Occupation**

124 *Connectivity and Population Dynamics*

125   At an operational level of supporting the lives of juvenile fish, nurseries comprise a complex

126   mosaic of interacting habitat units and the connectivities enabling their interaction (Sheaves

127   2009). The importance of juvenile habitat is well recognised, and is a key driver for the

128   identification of essential fish habitat in the USA (e.g. Froeschke et al. 2013) and Europe

129   (Vasconcelos et al. in press). However current definitions for identifying nursery habitats

130   emphasise the habitats which leave a distinctive chemical signature or are the habitats from

131   which juveniles can be most readily sampled (Gillanders 2005). This disregards the fact that

132   many aquatic species shift habitats during their time within the nursery (Kimirei et al. 2011),

133   and that other critical habitats might only be occupied transiently (Tupper 2007) or indirectly

134   support nursery value (Connolly et al. 2005).

135   *Connectivity (Fig. 1a)*: Ontogenetic habitat shifts, the use of transitory and temporary

136   habitats (Potter et al. in press), and the use of a mosaic of habitats within the nursery seascape

137   (Nagelkerken et al. in press) attest to the central importance of connectivity in supporting

138   nursery ground value (Vasconcelos et al. 2011). Yet connectivity is more than just the

139   movement of individuals among habitats; it is a facilitator that enables a variety of critical

140   ecological functions to support nursery value (Sheaves 2009). For instance, deriving maximal

141   nursery ground value relies on spatio-temporal matching between the functional requirement

142   to use the particular habitat (e.g. refuge), the occurrence of appropriate resources (e.g.

143   flooded marsh surface) and physical conditions in the habitat (e.g. oxygen levels), and it is

144   connectivity that allows this complex matching to occur. The facilitating role of connectivity

145   is pervasive (Beger et al. 2010), and it is a key factor supporting most ecological interactions

146   conferring nursery ground value.

147   *Ontogenetic migrations (Fig. 1b)*: Ontogenetic migrations occur at a range of scales, from

148   movements along freshwater to marine gradients (Russell and Garrett 1985, McBride et al.

149   2001, Davis et al. 2012), and movements within local habitat mosaics (Nagelkerken 2009,

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150   Grol et al. 2011). Local scale migrations include both easily identifiable meso-term habitat

151   shifts (e.g. seagrass to mangrove to patch reefs (Nagelkerken et al. 2000a)) and ephemeral

152   habitat occupancy (e.g. initial settlement habitats (Dahlgren and Eggleston 2000, Grol et al.

153   2011)) that is more difficult to detect. Not only do ontogenetic habitat shifts exist across a

154   range of dependencies, from facultative (Milton et al. 2008) to more obligate (Potter et al. in

155   press), but they may vary spatially (Kimirei et al. 2011). For instance, *Haemulon*

156   *flavolineatum*, one of the most common Caribbean ontogenetic shifters, moves from rubble

157   habitat to seagrass beds to mangroves to rocky substratum in some geographic locations

158   (Grol et al. 2011), but from rubble habitat to sea urchin spines to seagrass beds to lagoonal

159   patch reefs in others (Ogden 1988).

160   ***Seascape migrations (Fig. 1c)***: On shorter time scales, feeding migrations and movements to

161   refugia are vital facilitators of key nursery functions, and connect multiple habitats within the

162   nursery seascape (Sheaves 2005, Verweij and Nagelkerken 2007). In situations where large

163   tidal differences occur, intertidal habitats such as salt marsh or mangrove roots are only

164   available periodically (Minello et al. 2012), leading to regular tidal migrations. Even in cases

165   where tides do not play a major role, many organisms show predictable diurnal movements

166   between shelter habitats and foraging grounds (Hammerschlag et al. 2010). Seascape

167   structure, the spatial patterning of prey and predator species, and the hydrodynamics and

168   geomorphology of the ecosystem all play important roles in structuring such animal

169   movements across habitats (Nagelkerken 2007, Baker et al. 2013).

170   *Ecological and Ecophysiological Factors*

171   ***Ecotone effects (Fig. 1d)***: Ecotones are important contributors to nursery ground value.

172   Indeed, estuarine nurseries occur in transitional waters between freshwater reaches and the

173   sea and have been defined as traditional ecosystems in their own right (Basset et al. 2013).

174   Animal communities often show strong spatial patterning within the seascape, and it is

175   especially at the edges of habitats where highest species richness and densities are observed

176   (Dorenbosch et al. 2005, Johnston and Sheaves 2007). For example, fish densities in seagrass

177   beds can decrease with distance away from patch reefs (Valentine et al. 2008), and the

178   highest fish and crustacean densities are found at the seaward fringes of salt marsh (Minello

179   et al. 2003) and mangroves forests (Vance et al. 1996). As boundaries that need to be crossed

180   moving between habitats, ecotones are also areas where risks can be greatest (Hammerschlag

181   et al. 2010), and so are points where population structuring factors like predation focus can be

182   particularly influential (Sheaves 2005, Baker and Sheaves 2009b).

183   *Ecophysiological factors (Fig. 1e)*: Physical factors and physiological abilities are critical in

184   determining spatial (Sheaves 1996a, Harrison and Whitfield 2006) and temporal (Attrill and

185   Power 2004) patterns of nursery ground occupancy. This manifests at a diversity of scales;

186   for instance relating to ontogeny of habitat use (McBride et al. 2001), seasonal occurrence of

187   necessary physical conditions (Davis et al. 2012) and nutrients (Abrantes and Sheaves 2010),

188   long-term patterns of nursery utilisation (Sheaves 1998), variations in optimal nursery

189   habitats (Hurst and Conover 2002), or responses to multi-year climatic cycles (Sheaves et al.

190   2007). Consequently, in many systems nursery provision will change substantially over time

191   (Minello et al. 2012), providing advantage to different species under different conditions.

192   Differing behavioural and physiological abilities allow different species, and even different

193   ontogenetic stages, to access and use different nursery grounds or use nursery grounds in

194   different ways. Air breathing organs in species such as tarpon (*Megalops* spp.) allow them to

195   utilise hypoxic wetland nurseries (Seymour et al. 2008), while barramundi (*Lates calcarifer*)

196   juveniles are able to access hypersaline wetlands from which predators and competitors are

197   excluded (Russell and Garrett 1985). Even in deeper estuarine waters hypoxia can exclude

198   species from habitats during periodic hypoxic events (Pihl et al. 1991, Switzer et al. 2009). In

199   response, many estuary species can detect and avoid areas of low dissolved oxygen

200   concentration (Wannamaker and Rice 2000). Not only do different salinity preferences

201   contribute to nursery habitat partitioning by co-occurring juvenile fish (Davis et al. 2012), but

202   physical conditions can have substantial influences on growth rates of juveniles (Del Toro-

203   Silva et al. 2008), with salinity and temperature regimes often having more substantial

204   influences on growth than diet (Baltz et al. 1998). Eco-physiological effects can be complex,

205   interacting with ecological processes to effect changes in nursery value for different juvenile

206   stages. For instance, ecophysiological differences allow young juvenile California halibut,

207   *Paralichthys californicus*, to occupy estuaries with abundant prey and few predators from

208   which larger juveniles are excluded because of narrower salinity and temperature tolerances

209   (Madon 2002).

210   ***Food/Predation Trade-Offs (Fig. 1f)***: Juveniles utilising nurseries face a complex trade-off

211   between the need to obtain sufficient, appropriate prey, and minimising predation risk

212   (Sogard 1992, Baker and Sheaves 2007). This trade-off can profoundly affect nursery ground

213   value, and the quantity and quality of sub-adults migrating to adult habitats (Walters and

214   Juanes 1993, Kimirei et al. 2013). The need to access prey-rich areas can initiate or

215   necessitate behaviour that exposes juveniles to increased predation risk (Alofs and Polivka

216   2004, Sheaves 2005) or to forage in areas that support poor growth rates (Sogard 1992,

217   Harter and Heck 2006). In fact, the underlying mechanisms that drive habitat shifts are often

218   related to minimizing the ratio of mortality risk to growth rates (Werner and Hall 1988,

219   Halpin 2000), because profitable habitats for food acquisition are often riskier in terms of

220   probability of predator encounter (Hammerschlag et al. 2010). Predation is usually the largest

221   source of mortality for juvenile fish (Harter and Heck 2006), so high risk areas, such as

222   transition zones between refuge and feeding areas (Hammerschlag et al. 2010) may represent

223   ecological bottlenecks. For example, predatory activity at these locations can control the

224   supply of recruits to nursery grounds (MacGregor and Houde 1994, Brown et al. 2004) and

225   the supply of juveniles from nursery grounds to adult populations (Yurk and Trites 2000,

226   Friedland et al. 2012), and so provide the opportunity for predatory control of nursery

227   populations (Baker and Sheaves 2009b). In addition, these refuge-food acquisition trade-offs

228   vary between species (Camp et al. 2011) meaning that nursery ground values may differ

229   markedly depending on the species involved.

230   *Food webs (Fig. 1g)*: Predators have a strong top-down control on food webs. While

231   nurseries have typically been assumed to harbor few predators, recent studies have shown a

232   more complex picture (Baker and Sheaves 2009a, Dorenbosch et al. 2009). Although

233   standing stock of predators may be low much of the time, immigrating predators from

234   adjacent systems can produce profound predatory effects on nursery fish during their short

235   foraging forays (Baker and Sheaves 2009a). Moreover, many nursery species shift

236   ontogenetically to higher piscivory while still occupying nurseries (Baker and Sheaves

237   2009a). The spatio-temporal presence of predators and their specific gape sizes will

238   determine to what degree they control fish populations in nurseries. Secondly, interspecific

239   interactions may determine which species ultimately are responsible for greatest export to

240   adjacent ecosystems. Recruitment of nursery fish may be highly variable in time, and feeding

241   habitat and food availability may be limiting during nursery occupancy (Igulu et al. 2013).

242   Competitive exclusion from optimal foraging habitats among species may be an important

243   determinant of the winners and losers of nursery habitat use in terms of growth, survival, and

244   successful movement to consecutive habitats.

245   *Resource Dynamics*

246   The availability, distribution and quality of resources within the nursery are critical

247   parameters underpinning nursery ground value, the pattern of use of resources, and ultimately

248   the outcome of nursery ground residence. Resource use is complex, varying along stage-

249   specific, time-specific and purpose-specific axes.

250   ***Resource availability (Fig. 1h)***: Nursery grounds are often nutritionally rich ecosystems

251   maximizing cohort growth during nursery ground residence (Yanez-Arancibia et al. 1994),

252   and marine organisms invest heavily in rapid growth during their early life stages. Prey

253   quantity and quality affect growth (Sogard 1992, Scharf et al. 2006) because of substantial

254   differences in the energetic value of different prey types (Ball et al. 2007). Although fish may

255   be able to switch to alternative prey (Gartland et al. 2006), there are limits to this ability to

256   adapt (Nobriga and Feyrer 2008), and particular prey may be required at particular life stages

257   (Robertson and Duke 1990, Baker and Sheaves 2005). Consequently, the quality, quantity

258   and availability of food resources is an important factor in nursery value, although food

259   acquisition often necessitates trade-offs with predation avoidance (see above). High quality

260   nursery grounds are also those that provide optimal habitats relative to the full range of life-

261   history functions (Nagelkerken and van der Velde 2002, Nagelkerken et al. in press), such as

262   juvenile settlement (Dahlgren and Eggleston 2000, Grol et al. 2011), foraging (Nagelkerken

263   et al. 2000b, Harter and Heck 2006) and refuge (Ellis and Gibson 1995, Sheaves 1996b,

264   Gorman et al. 2009).

265   ***Ontogenetic diet shifts (Fig. 1i)***: Complex seascape dynamics, with juveniles obtaining

266   resources from different habitats during different phases of their nursery residence, mean that

267   the development of complicated and variable food webs is inevitable (Nagelkerken et al.

268   2006). Due to ontogenetic dietary shifts, many juveniles change their trophic identity during

269   nursery occupation. Profound changes in diet over development mean they may not even

270   participate in the same trophic web throughout nursery occupation. For example, juvenile

271   *Platycephalus fuscus* initially feed almost entirely on amphipods and so participate in a food

272   web based on benthic productivity, while larger juveniles in the same habitat switch to

273   feeding extensively on planktivorous fish (Baker and Sheaves 2005). Such ontogenetic diet

274   shifts are widespread among estuarine and coastal fishes (Elliott et al. 2007), and the

275   availability of the different food items that are preferentially selected through ontogeny is an

276   important driver of the realized growth during nursery occupancy.

277   *Allochthonous inputs (Fig. 1j)*: In marine systems water is an effective vector for the

278   movement of energy and nutrients among habitats, allowing substantial trophic subsidies that

279   affect the structure of animal populations in recipient systems (Deegan 1993). In some

280   situations, animals are sustained by food webs based on autotrophic production within their

281   habitat (e.g. juvenile fish in seagrass meadows in the Mediterranean (Vizzini et al. 2002), and

282   animals on saltmarshes in subtropical Australia (Guest and Connolly 2004)). Often, however,

283   nutrition is derived ultimately from plants or algae growing elsewhere. Organic matter from

284   seagrass meadows can sustain food webs in adjacent habitats (Heck et al. 2008), supporting

285   production in both temperate (e.g. Connolly et al. 2005) and tropical (e.g. Melville and

286   Connolly 2005) systems, while mangroves also have been shown to support fish production

287   in adjacent estuarine (Abrantes and Sheaves 2009a) or coastal waters (Bouillon et al. 2008) in

288   certain situations. Stable isotope analysis has demonstrated both the detrital pathway for this

289   transfer and the fact that movement of nutrients can also occur through in-welling from

290   coastal to intertidal waters (Connolly et al. 2005).

The Support of Recipient Populations and Ecosystems by Nursery Grounds

292   The conventional view of nursery ground value (e.g. Heck et al. 1997, Beck et al. 2001)

293   emphasises the contribution of juveniles from inshore nurseries to recipient (usually offshore)

294   populations, and its crucial role in supplying adult populations with new individuals. The

295   migration of juveniles also represents the biologically-mediated export of nutrients,

296   incorporated into juvenile biomass during nursery residence, donated to offshore systems

297 (Deegan 1993, Beck et al. 2001). The export of biomass was suggested by Beck et al. (2001)

298 to be the best integrative measure of the contribution of juveniles to future generations.

299 However, the numbers and biomass of individuals that reach adult stocks represent only part

300 of the contribution that juveniles using nursery grounds make to recipient populations and

301 ecosystems (Fig. 1, 2).

302 *Diverse trophic contributions*: From the moment of recruiting to the nursery ground the

303 abundance of a cohort is continually and exponentially pruned back by mortality (Yanez-

304 Arancibia et al. 1994, Doherty et al. 2004). As abundance declines individual biomass

305 increases until a very small number (relative to those recruiting) of large individuals emigrate

306 from the nursery ground (Yanez-Arancibia et al. 1994, Sheaves et al. 2013) transferring their

307 accumulated biomass to offshore habitats (Deegan 1993), where they may be ultimately

308 measured as contributing to adult stocks (Beck et al. 2001) (Fig. 2a). However, most

309 individuals, and a significant proportion of the biomass, do not survive to emigrate (Deegan

310 1993, Yanez-Arancibia et al. 1994, Baker et al. 2014) and so do not figure in calculations of

311 exported biomass. However, these individuals are critical to nursery ground value by

312 forming what is essentially a sacrificial nursery component that allows other nursery

313 individuals to survive (Sandin and Pacala 2005, Svenning et al. 2005) (Fig. 2b). In doing so,

314 they provide food for juvenile predators within the nursery (Minello et al. 1989, Baker and

315 Sheaves 2005) (Fig. 2c) that ultimately translocate accumulated nutrients offshore during

316 their ontogenetic migrations (Thorson 1971, Werry et al. 2011) (Fig .2a), and for transient

317 predators from offshore feeding within the nursery (Begg and Hopper 1997) that return

318 offshore exporting biomass accumulated in the nursery ground (Fig. 2d). These juveniles also

319 form critical links in nursery food webs (Abrantes and Sheaves 2009a, b) (Fig. 2e), provide a

320 vehicle for transferring production among habitats (Rozas and LaSalle 1990), and form

321 critical components of trophic relays where intermediate prey link production sources in one

322   habitat with higher consumers in another (Kneib 1997) (Fig. 2f). When viewed this way, the

323   nursery cohort is largely made up of individuals comprising a critical resource in the trophic

324   functioning of the nursery and adjacent connected ecosystems, with the survivors

325   representing surplus individuals not consumed in powering the system. Valuing a nursery

326   based only on the biomass of individuals that reach adult stocks clearly overlooks a diversity

327   of processes critical to the function of these systems (Sheaves et al. 2006) because the relative

328   contributions from different nurseries of individuals that ultimately reach the adult stocks

329   does not reflect the full production output of each nursery or their contributions to the support

330   of other species. Although specifically quantifying all the components of biomass transfer

331   will rarely be practical given our current knowledge bases, quantification is not the primary

332   issue. Recognising that the true value of trophic contributions from nursery grounds is much

333   more extensive than can be measured as exported biomass alone is critical for the effective

334   management of nursery function, and to developing approaches to begin to quantify those

335   additional contributions.

336

337   *Export of process*: The influence of nursery grounds on offshore ecosystems is not confined

338   to the contribution of individuals to adult populations or biomass translocation, but extends to

339   effects on key processes in the recipient ecosystems (Fig. 2g). Connectivity to mangrove

340   nursery grounds influences overall community structure and resilience on many Caribbean

341   coral reefs. Because dominant herbivores have an obligate mangrove nursery phase the

342   presence of mangroves has a substantial impact on the numbers of herbivores on adjacent

343   reefs, thus regulating the beneficial effects of herbivory in those systems (Mumby et al.

344   2004), and greatly increases resilience of mid-shelf reefs to severe hurricane disturbances

345   (Mumby and Hastings 2008). At the other end of trophic webs, as well as contributing to the

346   export of biomass, the movement of juvenile bull sharks, *Carcharhinus leucas*, from coastal

347 nurseries (Curtis et al. 2011, Heupel and Simpfendorfer 2011) represents the supply of sub-

348 adult and adult high-level predators (Marshall and Bennett 2010) that can be major influences

349 on offshore predation dynamics (Hunsicker et al. 2012) and severely impact lower trophic

350 levels through trophic cascades (Myers et al. 2007). The export of process extends to

351 biological controls, with juvenile grouper from mangrove nurseries having the potential to

352 control populations of invasive lionfish on Caribbean coral reefs (Maljkovic et al. 2008). The

353 growing awareness of the complexity of interactions between different environmental realms

354 and the importance of connectivities at all scales in supporting ecological functioning (Beger

355 et al. 2010) suggests that many more effects of nurseries on ecological processes in recipient

356 ecosystems are likely to be recognised as our understanding of linkages between ecosystems

357 becomes more sophisticated. As with developing a more complete understanding of the

358 spectrum of contributions from trophic interactions, developing a more complete

359 understanding of the process links emanating from nursery grounds to influence recipient

360 ecosystems is critical to developing a comprehensive understanding of the true value of

361 nursery grounds.

Current situation: Approaches available to identify the full value of nurseries

364 The value of any juvenile habitat depends on its complex contributions to the sustainability of

365 populations and the functioning of replenishing and recipient ecosystems. Recognising the

366 lack of a framework for identifying valuable nurseries, Beck et al. (2001) proposed an

367 approach to rank nursery grounds based on the total biomass contributed from different

368 putative nursery habitats. This was an important advance, recognising the need to compare

369 contributions across all possible nursery habitats. However, this is only a first step, because

370 comprehensive identification, valuation and management of estuarine and coastal nurseries

371 for fish requires detailed understanding of the range of processes supporting nursery value

372 (Jones et al. 2002), and of the full value of outputs to recipient ecosystems (Mumby and

373 Hastings 2008). Additionally, while ranking nurseries may provide guidance for prioritising

374 areas for conservation very broadly, it is of limited value for managers charged with

375 maintaining nursery function in the face of impacts at specific locations. The increasingly

376 urgent need to understand and maintain ecosystem function across the globe is driven far

377 more by the need to manage ever-increasing anthropogenic impacts, and multiple coastal

378 users with conflicting usages, to our environment than by a desire to totally protect functional

379 ecosystem units. It would be better, therefore, if protection and management of nursery

380 grounds is not based solely on a ranking of the relative value of different putative nurseries.

381 The approach we are recommending aligns with the broader shift to managing marine

382 systems to conserve ecosystem functioning rather than focusing on individual species or

383 habitat units (Foley et al. 2010).

384 Determining the relative contributions of putative nurseries to adult stocks in terms of

385 numbers or biomass can often be achieved via retrospective determination of movement of

386 individuals from particular nurseries to the adult population using artificial or natural markers

387 (Gillanders et al. 2003, Gillanders 2005). For example, otolith chemistry may distinguish

388 occupation of one coastal bay or estuary rather than another (Yamane et al. 2010, Reis-Santos

389 et al. 2012), or differentiate between use of particular salinity zones (Albuquerque et al. 2012,

390 Webb et al. 2012), or distinguish use of particular seascape components (Gillanders and

391 Kingsford 1996). However, while natural markers can be used to define spatial units

392 contributing most biomass to recipient adult populations, they are really only able to identify

393 areas that can be most easily distinguished (e.g. ones that leave an otolith chemical

394 signature), and are unlikely to be able to identify important habitats occupied for short

395 periods (e.g. initial settlement habitats (Dahlgren and Eggleston 2000, Grol et al. 2011)),

396   habitats that are used intermittently (foraging and sheltering habitats (Sheaves 2005, Verweij

397   et al. 2007)), and linkages and pathways among habitats (Nagelkerken 2007, Hammerschlag

398   et al. 2010). Moreover, they provide little information on how habitats are used or on the

399   processes and functions (e.g. food web resilience or resource dynamics) that are critical to

400   nursery value but are not specifically related to a particular spatial unit.

401   There are also practical limitations to the use of ranking based on the contribution of spatial

402   units. As well as providing scant information on process, approaches such as otolith

403   microchemistry frequently do not allow identification of juvenile habitats at the scale where

404   key processes operate, the scale used by the juveniles themselves, or at a scale amenable to

405   management action (Gillanders et al. 2003). It will often not be feasible for management to

406   protect the entire unit identified; all of one bay, all of one salinity zone or all of one seascape

407   component. As a result, managers will often seek to minimize impacts within the unit

408   identified as a nursery. However, many supporting processes and negative impacts arise well

409   beyond a specific unit of habitat, so unless the specific values and supporting processes of

410   particular sub-units and connectivities are known, such spatial prioritization is likely to fail.

411   Ranking of nurseries assumes that nursery components have independent contributions to

412   nursery value (Beger et al. 2010). However, the complex nature of nursery ground provision,

413   with multifaceted interactions transcending individual spatial units, means that identification

414   of nursery habitat cannot be approached as a static process in which individual habitats and

415   life phases are singled out. Ignoring these interactions could be justified when it is possible to

416   conserve a whole ecosystem (e.g. whole estuary or whole of coastal seascape) containing all

417   units contributing to nursery function; as is the case with large protected areas. More often,

418   management will need to work with much more specific units. The ranking process then

419   provides little help, and may even be misleading because it suggests that one area can be

420   protected at the expense of others. Even if ranking could be achieved at an appropriate scale

421   to enable relative valuation of different spatial units, it intrinsically disregards the critical

422   importance of interactions among ensembles of habitat units (Sheaves 2009, Grol et al. 2011),

423   the importance of connectivity among the habitat units (Beger et al. 2010), and the

424   importance of habitats only occupied transiently (Nagelkerken et al. in press).

Solutions: Approaches available to identify the true value of nurseries

426   Determining how nursery value is influenced by connectivity, habitat type, habitat diversity,

427   ecological interactions and trophic process seems like a complex task, but the type of

428   information needed is already being collected; it just needs to be recombined, extended and

429   refocused specifically on understanding nursery function. Not only can particular techniques

430   contribute to understanding different aspects of nursery value (columns of ticks in Table 1)

431   but combining various approaches can provide rich and extensive detail on specific aspects of

432   nursery value (rows of ticks in Table 1).

433   To illustrate: connectivity studies using natural and artificial markers are becoming the

434   principal techniques for determining biomass or numeric contributions from alternative

435   nurseries to adult stocks (see above). However, marker studies have broader applicability

436   (Table 1). Not only can they provide valuable inputs to understanding of nursery values

437   ranging from ontogenetic migration to export of process but, when combined with other

438   techniques, can contribute to a much deeper understanding of many aspects of nursery value.

439   For example, combined with data including food web and fish-habitat relationship

440   information, gleaned from stable isotope, dietary, observational and capture studies, they can

441   provide information on ontogenetic migration, seascape migration, ecotone effects and

442   connectivity itself (Table 1: rows 1a-2a). Similarly, contributions to juvenile predator

443   biomass can be informed by: stable isotope and dietary studies used to define nursery food

444   webs; dietary, observational, capture and tethering studies supplying information on predator

445   identification and dynamics; and energetics and condition studies determining juvenile

446   growth and health (Table 1: row 4d).

447   Many other solutions are indicated in Table 1. These are far from exhaustive and a variety of

448   other possibilities and combinations of approaches are likely to be fruitful. In particular, it

449   will usually be possible to define more specific detail when the ideas are applied to particular

450   cases and the studies are considered in explicit spatial and temporal contexts. The

451   possibilities of the information that can be gleaned using multiple techniques should expand

452   quickly as new combinations of approaches are successfully applied to new problems.

453   **Conclusion**

454   A historical analysis of nursery-function studies shows progressive development of this

455   important field: (1) the recognition that inshore habitats harbor high densities of juvenile fish

456   (1970s; e.g. Weinstein 1979)), (2) the study of community structures of individuals nursery

457   habitats (1980s; e.g. Robertson and Duke 1987), (3) the quantification of consecutive habitat

458   usage by different life stages of fish (1990s; e.g. MacPherson 1998), (4) development of

459   conceptual frameworks that identify critical nursery habitats (2000s; e.g. Beck et al. 2001),

460   (5) recent studies that have used these frameworks in a quantitative way to identify primary

461   nursery habitats (Tupper 2007, Huijbers et al. 2013). We are now at a stage where we need to

462   take a step forward, building on these advances by developing an understanding of the

463   processes that drive the productivity and maintenance of these identified key nurseries, and to

464   go beyond valuation based simply on export of number or biomass, by incorporating the

465   complex of factors that contribute to nursery value to provide a more comprehensive

466   understanding of true nursery value. Only through this comprehensive understanding can we

467   confidently identify the habitat mosaics and underlying connectivities/processes that are

468   important to conserve to maintain nursery production and replenishment of recipient

469   ecosystems. Ongoing degradation of coastal ecosystems increases the imperative for more

470   complete understanding. Rapid loss of nursery habitats and escalating habitat fragmentation

471   increase the pressure to conserve critical habitats and maintain ecosystem function. The

472   identification of nursery habitats at a whole of habitat-unit scale, as is currently advocated,

473   will not suffice in fragmented seascapes or in the face of specific impacts at particular

474   locations. Consequently, an understanding of the complex processes that underlie nursery

475   function is needed to support selection of appropriate fragments that can still provide key

476   nursery functions. Failure to incorporate this complexity into conservation approaches and

477   reserve design risks incomplete or inaccurate identification of key habitats and connectivities,

478   and leads to significant potential for unexpected negative outcomes (Harris and Heathwaite

479   2012). Our current perspective provides a conceptual framework that can aid progress

480   towards more complete understanding of nursery ground value, utilising data that are already

481   available in the literature. It is only by continuing development of detailed understanding of

482   the true value of nursery grounds and their functioning that we can hope to effectively protect

483   these systems into the future.

484

Acknowledgements

488

Figure Captions

490 Figure 1: Components of Nursery Ground Value. Each component is described and discussed
491 in the text.

492 Figure 2: Support of recipient ecosystems from nursery grounds is more than just export of
493 new individuals to adult stocks and the biologically mediated nutrient translocation they
494 represent (a). Individuals lost through mortality within the nursery facilitate the survival of
495 those that ultimately emigrate (b), as prey participate in the continued transfer of biomass to
496 local (c) and immigrating predators that feed in the nursery and subsequently move to
497 recipient habitats transferring biomass (d), form important prey and critical links in food

webs that support nursery value (e), contribute to trophic relays as they are fed on during
emigration (f), and influence key processes in recipient ecosystems (g).

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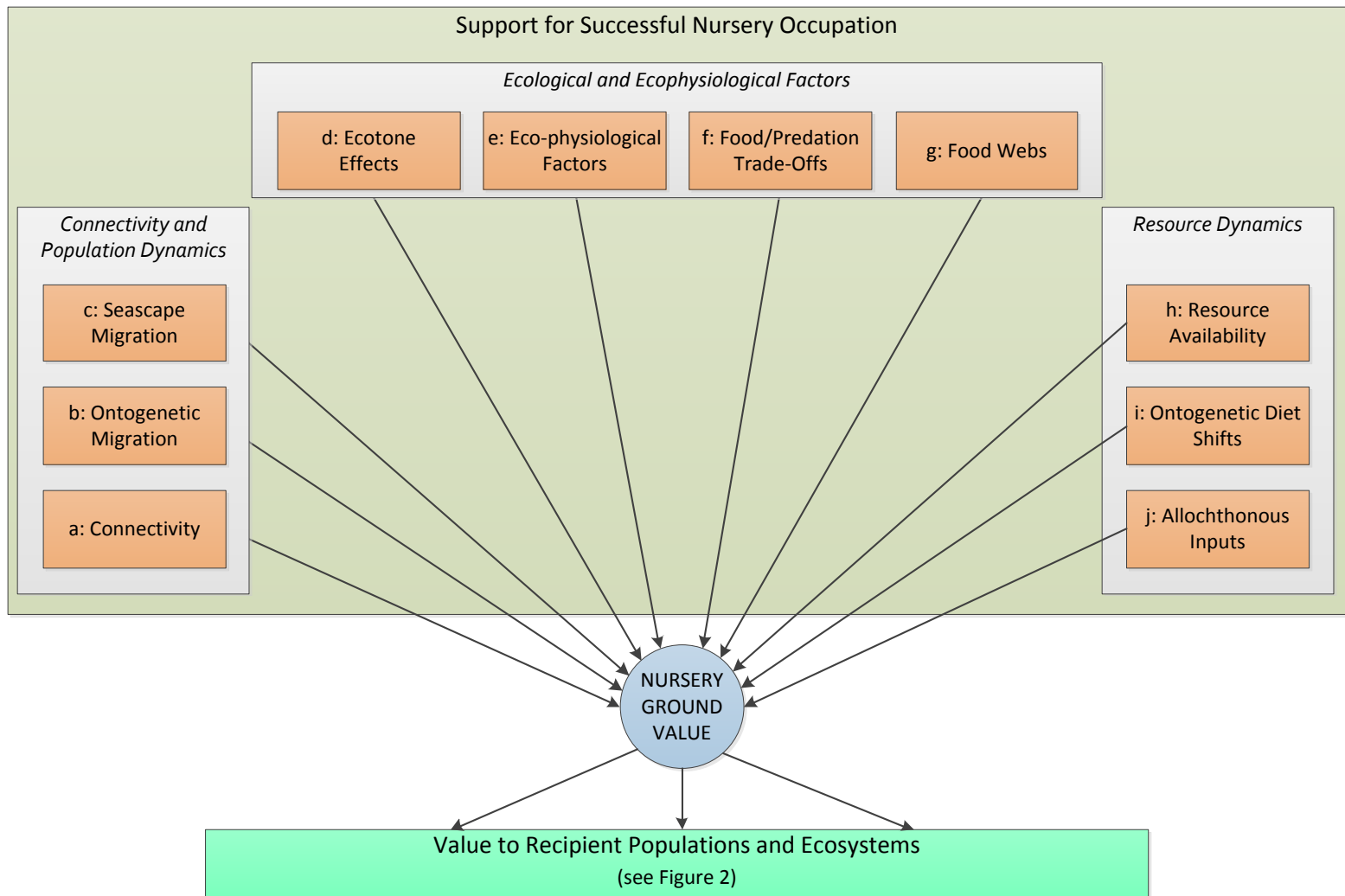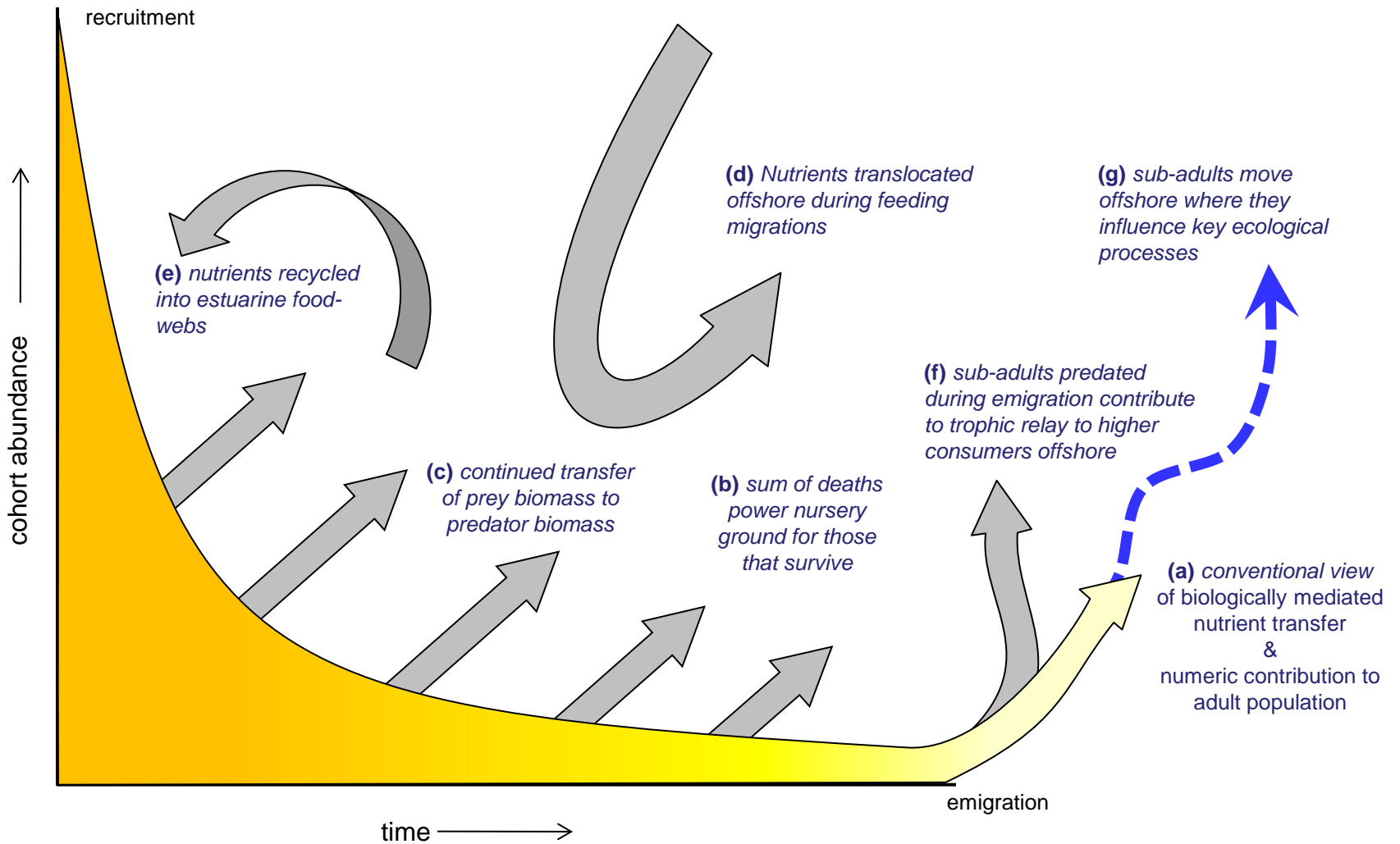864 129:1360-1366.

Figures

Figure 1

recruitment

cohort abundance

(e) *nutrients recycled into estuarine food-webs*

(d) *Nutrients translocated offshore during feeding migrations*

(g) *sub-adults move offshore where they influence key ecological processes*

(f) *sub-adults predated during emigration contribute to trophic relay to higher consumers offshore*

(c) *continued transfer of prey biomass to predator biomass*

(b) *sum of deaths power nursery ground for those that survive*

(a) *conventional view* of biologically mediated nutrient transfer & numeric contribution to adult population

emigration

time

Figure 2

Table

Contributions to Understanding

	nursery value	temporal scale	spatial scale	connectivity	nursery food webs	fish-habitat relationships	juvenile population dynamics	target species diet	target species refuge ecology	habitat availability & condition	prey dynamics	predator identification & dynamics	nutrient dynamics	juvenile growth & health	environmental requirements	receiving food webs	receiving ecosystem function
1a	connectivity	all	all	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓				
1b	ontogenetic migration	life-history	mosaic	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓		
1c	seascape migration	short-meso	local	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓		
1d	ecotone effects	short	local	✓	✓	✓		✓	✓	✓	✓						
1e	eco-physiological factors	life-history	mosaic												✓		
1f	food/predation trade-off	short	local	✓		✓	✓	✓	✓	✓	✓		✓	✓			
1g	food webs	all	local	✓	✓							✓					
1h	resource availability	all	all	✓	✓	✓		✓	✓	✓	✓		✓				
1i	ontogenetic diet shifts	life-history	all	✓	✓			✓			✓		✓				
1j	allochthonous inputs	life-history	mosaic	✓	✓			✓			✓		✓				
2e	nutrients recycled into estuarine food webs	short-meso	local		✓								✓				
2a	biomass contribution to adult stock	life-history	mosaic	✓		✓											
2b	sacrificial nursery component	life-history	mosaic				✓					✓					
2c	contribution to juvenile predator biomass	life-history	mosaic		✓							✓		✓			
2d	contribution to visiting predator biomass	short	mosaic		✓							✓					
2f	trophic relay	meso	mosaic	✓	✓						✓	✓				✓	
2g	export of process	life-history	mosaic	✓												✓	✓
Study Types				natural & artificial markers	stable isotope & dietary	observational & capture	capture	dietary	observational & behavioural	habitat survey & acoustic	capture & acoustic	dietary, observational, capture, tethering	water & sediment chemistry, stable Isotope	energetics & condition	eco-physiology	stable isotope & dietary	integrated ecological studies

Left-margin group labels:
- Rows 1a–2e: **Support for Nursery Occupation**
- Rows 2a–2g: **Support of Recipient Ecosystems**