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REVIEW

Evidence of connectivity between juvenile and adult habitats for mobile marine fauna: an important component of nurseries

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ABSTRACT: A critical link missing from our understanding of the nursery role of specific marine habitats is the evidence of connectivity between juvenile and adult habitats. This paper reviews and evaluates evidence of, and spatial scales for, movements from juvenile to adult habitats and it summarises the methods used to study movements. Examples include many fish families but few invertebrate taxa, and most are species of economic importance for USA and Australia. The types of juvenile habitat range from the entire estuary or shallow open coastal waters to specific habitats within estuaries or coastal waters; in some cases juvenile habitats include habitats not traditionally regarded as nursery areas (e.g. the surf zone). The duration of time spent in juvenile habitats averages 13 mo (range 8 d to 5 yr). The majority of organisms move distances of kilometres to hundreds of kilometres from juvenile to adult habitats, although the scale of movements ranged from metres to thousands of kilometres. Changes in abundance among separate habitats and the progression of size classes among separate habitats are the main methods used to infer movement and habitat connectivity. Spatial partitioning of stages of maturity, natural parasites, and a variety of artificial tagging methods have also been used. The latter will become more useful with continued developments in the miniaturisation of artificial tags. More recent studies have used natural tags (e.g. trace elements and stable isotopes) and these methods show great promise for determining movements from juvenile to adult habitats. Few studies provide good evidence for movement from specific juvenile habitats to adult habitats. Future studies need to focus on this movement to supplement data on density, growth and survival of organisms in putative nursery habitats. Such information will allow management and conservation efforts to focus on those habitats that make the greatest contribution to adult populations.

KEY WORDS: Nursery habitat · Adult habitat · Movement · Spatial scale · Temporal scale · Estuary · Open coast · Review · Connectivity

INTRODUCTION

Organisms, organic matter and nutrients are transferred between a variety of habitats, for example, between freshwater and the ocean via estuaries, pelagic and nearshore coastal waters, and kelp beds, seagrasses and rocky reefs (Fairweather & Quinn 1993). Links between these habitats are most often viewed in terms of larval recruitment processes that transport propagules from pelagic to benthic environments (Underwood & Fairweather 1989, Fairweather 1991) or as trophic transfers or relays (e.g. Kneib 1997). In a

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*Email: bronwyn.gillanders@adelaide.edu.au review of linkages between different parts of the sea, however, Fairweather & Quinn (1993) highlighted the fact that there are relatively few studies of movement processes that link different habitats. In part, lack of studies may be due to the difficulty of tracking organisms between aquatic habitats, especially small propagules and juveniles. The potentially large spatial scale over which some linkages occur, and the fact that these linkages may be episodic and thus difficult to study, also accounts for the relatively few studies.

The horizontal transfer of organisms from juvenile to adult habitats can result in substantial movement of biomass, nutrients and energy (Deegan 1993). For example, approximately 5 to 10% of the total annual primary production of estuarine areas is exported to surrounding coastal and offshore habitats (Deegan 1993). Due in part to this high potential for export of biomass, estuarine habitats, such as seagrass meadows, marshes and mangrove forests, are frequently cited as nursery habitats. Generally, a habitat has been identified as a nursery if juvenile fish or invertebrate species occur at higher densities, suffer lower rates of predation or have higher rates of growth in this habitat than in other habitats (Beck et al. 2001). However, these criteria have not addressed whether these juvenile habitats successfully transfer the higher juvenile biomass to the adult populations (Beck et al. 2001).

Following Beck et al. (2001), a habitat is considered a nursery for juveniles of a particular species if its contribution per unit area to the production of individuals that recruit to adult populations is greater, on average, than production from other habitats in which juveniles occur. Beck et al. (2001) suggested that it is critical to measure the movement of individuals from juvenile to adult habitats, and that this is a vital missing link in our understanding of nurseries. The purposes of our paper are (1) to review and evaluate evidence for movements from juvenile to adult habitats, (2) to evaluate methods that have been used to determine this movement, and (3) to provide information on the spatio-temporal scales of such movement. In particular, we assessed whether or not evidence exists to suggest that organisms move from any of the so-called nursery habitats (e.g. marshes, mangroves and seagrasses) to adult habitats, and describe the spatial scales over which these habitats are linked via dispersal.

METHODS

The nursery role hypothesis as stated by Beck et al. (2001) only relates to species that have at least some spatial disjunction between juvenile and adult habitats (Fig. 1). We have limited our review to such species. Juvenile habitats are areas that are used for some period of time by juveniles prior to movement to adult habitat. Adult habitats are considered to be areas where juveniles are not found and may encompass sub-adult staging areas. Movement from juvenile to adult habitats is usually associated with reproduction or an ontogenetic or seasonal habitat shift probably due to changing ratios of mortality risk to growth rate (Gilliam & Fraser 1987, Dahlgren & Eggleston 2000). Some juvenile habitats may fit the definition of nursery habitats. However, in this review we make no distinction between juvenile and nursery habitats because there is typically insufficient data to make this distinction (Beck et al. 2001).

We searched Aquatic Sciences and Fisheries Abstracts (Cambridge Scientific Abstracts) for the period January 1982 to October 2000 using a combination of keywords: (1) movement or migration and (2) nursery, juvenile, fish, shrimp, crab, prawn or decapod. From these searches plus our personal libraries, relevant publications that dealt with movement of organisms from juvenile to adult habitats were examined. We have generally avoided citing unpubl. papers and those in the 'grey' literature, as these are difficult to obtain and generally not available to most readers.

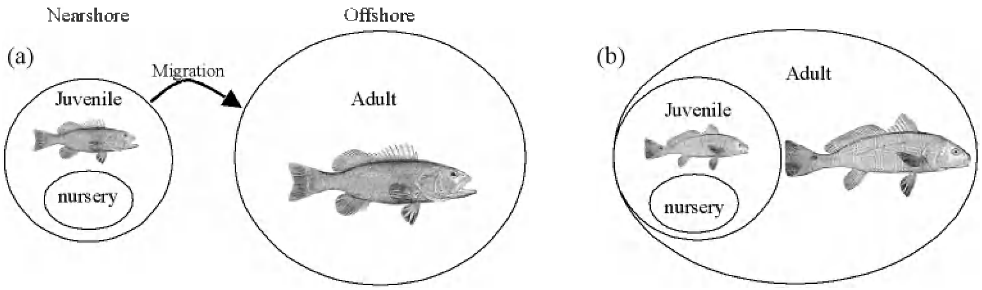

Fig. 1. Relationship between juvenile, nursery, and adult habitats. The ovals represent the portions of habitats used during juvenile and adult stages. Nursery habitats are a subset of juvenile habitats. (a) Classic concept of species that have nursery habitats, and (b) general concept of species that have nursery habitats. From Beck et al. (2001), published with permission. Copyright, American Institute of Biological Sciences

Of the papers that met the above criteria, some were missing data that would have assisted our analyses (e.g. length of time in nursery habitats, spatial scale of movement). We have included papers in the review even if they only provide information on, for example, the length of time in the nursery habitat and no information on the spatial scale of movement. However papers were not included in the review if the distribution and population dynamics of all stages of the life history of individual species were not examined in the same study.

RESULTS AND DISCUSSION

Species with separate juvenile and adult habitats

A total of 110 studies fit our criteria and were included in this review. Most of the studies (98 %) showing movement from juvenile to adult habitats focused on fish (n = 67) or decapod crustaceans (n = 41; see Table 1). The majority of studies (78 %; n = 41) examining movement of crustaceans were limited to the economically important penaeid shrimps and palinurid lobsters (e.g. Costello & Allen 1966, Fry 1983, Booth 1986, Staples & Vance 1986). Studies focusing on fish covered a wide range of families (e.g. Clupeidae, Labridae, Paralichthyidae, Pleuronectidae, Salmonidae, Sciaenidae, Sparidae), but again most species were of economic value. The queen conch *Strombus gigas* (Gastropoda), which moves from shallow sand and seagrass habitats to deeper seagrass, sand and algal habitats, was the only mollusc for which evidence of spatially segregated juvenile and adult habitats was found (Stoner et al. 1988, Stoner 1989).

Of the 110 papers reviewed, over 60 % of the studies were conducted in the Northern Hemisphere; these studies covered a range of latitudes. In the Southern Hemisphere, however, almost 50 % of studies were conducted in the 10° latitude band between 30 and 40°S. Within each hemisphere the majority of studies have been conducted in one country; Australia or USA. Few studies were conducted in Europe, Asia, South America or Africa (but see Benfield et al. 1990, Abello & Macpherson 1991, Koutsikopoulos et al. 1995, Roa et al. 1995, Griffiths 1996, Yamashita et al. 2000).

Types of juvenile habitat ranged from those traditionally viewed as 'nursery' habitats—the entire estuary or specific habitats within estuaries (e.g. mangroves, marshes, seagrasses)—to habitats outside of estuaries, such as the surf zone along sandy beaches and sulphide microbial communities (Table 1). Most adult habitats were in coastal waters offshore of estuaries and included reefs, offshore regions and the continental shelf. Specific habitats within estuaries or coastal regions were not often identified.

Methods for determining movement

A variety of methods has been used to determine movement from juvenile to adult habitats (Table 2). These methods generally involve identifying changes in size- or age-structure of organisms in different habitats or sites over time either as individuals or as a group. Intrinsic (related to the real nature of the organism) and extrinsic (dependent on external circumstances) methods for measuring movement have been used (Buckley & Blankenship 1990). Extrinsic methods may be either external, such as external tags, fin clips, external parasites, or internal, such as tags, marks or parasites that are completely enclosed within the tissues of the organism. Movement can only be measured directly by observing individually recognised or tagged organisms shifting from one place to another. Though direct measurements are preferred, much of the information on movement of juveniles comes from indirect sources, including differences in distribution, abundance and size structure, and differences in physical stages of maturity (e.g. Eggleston 1995).

Distribution, abundance and size structure

A total of 101 studies suggest movement from juvenile to adult habitats. A majority of these studies (55 %) relied on changes in abundance among separate habitats or a progression of size classes among the separate habitats to document movement (Table 2). However, there are many problems associated with measuring movement using these methods. One such problem is under-sampling of the juvenile and adult habitats. For example, some studies have sampled only one location in each of the juvenile and adult habitats and have assumed a size progression between the 2 habitats. In other studies, only one type of juvenile habitat (e.g. seagrass) has been sampled and there is no information on whether juveniles may also occur in other habitats including part of the adult habitat (but see Gillanders 1997b). An exception to this general trend was the work of Deegan (1990) who sampled 4 locations in juvenile habitat (marsh) and 4 locations in adult habitat (open bay). Deegan (1990) found that density of Gulf menhaden *Brevoortia patronus* was highest in tidal creeks (average fish length 30–40 mm) and that abundances in creeks declined when fish grew to 45–50 mm, when they likely moved to open bay areas and then offshore.

The fact that organisms have frequently been collected using different methods in each of the juvenile and adult habitats is another problem (e.g. Deegan 1990) because gear biases may influence the data. It is, however, acknowledged that the different physical

Table 1. Examples of organisms with spatially segregated juvenile and adult habitats and the spatial scales over which they move from juvenile to adult habitats. Numbered sources are indicated in footnote below. na: not available

Common name	Scientific name	Spatial scales of movement (m)						Juvenile habitat	Adult habitat	Source
		10^0	10^2	10^3	10^4	10^5	10^6			
Queen conch	*Strombus gigas*	—						Shallow sand and seagrass	Deeper seagrass, sand, and algal plains	1, 2
Rockfish	*Sebastes* spp.	—						Surface canopy of kelp	Bottom habitats (9–13 m)	3, 4
Canary rockfish	*Sebastes pinniger*	—						Pelagic, shallow waters	Deeper water	4
Opaleye	*Girella nigricans*	—						Intertidal	Kelp forests	4, 5
Halfmoon	*Medialuna californiensis*	—						Offshore	Kelp forests	4
Kelp bass	*Paralabrax clathratus*	—						Shallow water among kelp	Deeper water	6
Spotty	*Pseudolabrus celidotus*	—						Shallow reef	Deeper reef	7
Banded morwong	*Cheilodactylus spectabilis*	—						Shallow reef	Deeper reef	8
Bocaccio	*Sebastes paucispinis*	—	—					Kelp forests	Deeper water	4
Spiny lobster	*Panulirus argus*			—				Shallow mangrove	Coral, sand, rock rubble	9
Ornate spiny lobster	*Panulirus ornatus*			—	—	—		Deep reefs (~19m)	Shallow reefs (<10–15 m)	10, 11
Northern pike	*Esox lucius*			—				Upstream of river estuaries	Estuaries	12
Ide	*Leuciscus idus*			—				Upstream of river estuaries	Estuaries	12
Burbot	*Lota lota*			—				Upstream of river estuaries	Estuaries	12
European perch	*Perca fluviatilis*			—				Upstream of river estuaries	Estuaries	12
Roach	*Rutilus rutilus*			—				Upstream of river estuaries	Estuaries	12
Grayling	*Thymallus thymallus*			—				Upstream of river estuaries	Estuaries	12
Western rock lobster	*Panulirus cygnus*			—	—			Limestone reef (<10 m)	Offshore waters (30–150 m)	13
Jinga shrimp	*Metapenaeus affinis*			—	—			Estuarine marshes	Offshore waters	14
Brown shrimp	*Penaeus aztecus*			—	—			Estuarine marshes	Offshore waters	15, 16
Brown tiger prawn	*Penaeus esculentus*			—	—			Seagrass (<2.5 m)	Deeper water	17
Banana prawn	*Penaeus merguiensis*			—	—			Mangrove estuary	Offshore waters	18, 19, 20
Mud crab	*Scylla serrata*			—	—			Estuaries	Open bay	21
Gag grouper	*Mycteroperca microlepis*			—	—			Seagrass	Nearshore reefs	22
Blue groper	*Achoerodus viridis*			—	—			Seagrass	Nearshore rocky reef	23, 24, 25
Nassau grouper	*Epinephelus striatus*			—	—			Shallow macroalgal meadows	Offshore coral reefs	26
School prawn	*Metapenaeus macleayi*				—			Estuaries	Nearshore waters	27
White prawn	*Penaeus indicus*				—			Estuaries	Offshore waters	28
Caramote prawn	*Penaeus kerathurus*				—			River estuaries (<15 m)	Offshore waters (>25 m)	29
Eastern king prawn	*Penaeus plebejus*				—	—		Estuaries (<6 m)	Nearshore waters	30, 31
Green tiger prawn	*Penaeus semisulcatus*				—			Bare substrate in bays (~10 m)	Offshore waters (25–50 m)	32
Dungeness crab	*Cancer magister*				—			Intertidal estuaries, shallow sandy waters	Subtidal estuaries, sandy coast	33
Barramundi	*Lates calcarifer*				—	—		Coastal swamps and tidal creeks	Estuaries, nearshore waters, adjacent streams	34, 35
California halibut	*Paralichthys californicus*				—			Estuaries and shallow sandy coast	Sandy coast and shelf	36, 37
English sole	*Pleuronectes vetulus*				—			Estuaries and shallow sandy coast	Sandy coast and shelf	38, 39
Yellowtail rockfish	*Sebastes flavidus*				—			Estuaries	Open coast	40
Flathead mullet	*Mugil cephalus*				—			Shallow banks of estuaries	Streams, estuaries and beaches	41
Sole	*Solea solea*				—	—		Brackish and estuarine waters	Offshore waters	42, 43
Tailor/bluefish	*Pomatomus saltatrix*				—			Estuaries	Sandy nearshore coast	44
Green rock lobster	*Jasus verreauxi*				—	—	—	na	na	45, 46
Pink shrimp	*Penaeus duorarum*				—	—		Estuaries and shallow coast	Offshore waters	47, 48
Blue crab	*Callinectes sapidus*				—	—		Shallow, vegetated estuaries	Deep, unvegetated estuaries	49
Spider crab	*Maja squinado*				—	—		Coastal kelp forest (<15 m)	Deep offshore water (40–60 m)	49

Table 1 (continued)

Common name	Scientific name	Spatial scales of movement (m)						Juvenile habitat	Adult habitat	Source
		10^0	10^2	10^3	10^4	10^5	10^6			
Atlantic menhaden	*Brevoortia tyrannus*				▬	▬		Estuaries	Offshore waters	50
Baltic flounder	*Platichthys flesus*				▬	▬		River and nearshore tidal mudflats	Offshore waters	51
Jackass morwong	*Nemadactylus macropterus*				▬	▬		Shallow bays and inlets	Middle and outer continental shelf	52
Tropical shad	*Tenualosa macrura*				▬	▬		Shallow coastal waters	Sheltered coastal waters	53
Australian salmon	*Arripis truttaceus*						▬	Shallow bays and estuaries	Exposed beaches and surge zones	54
Atlantic salmon	*Salmo salar*				▬	▬	▬	Rivers	Oceans	55
Pacific salmon	*Onchorhynchus* spp.				▬	▬	▬	Freshwater streams and estuaries	Nearshore and offshore waters	56, 57, 58

Sources: 1, 2: Stoner et al. (1988), Stoner (1989); 3: Carr (1991); 4: Carr & Reed (1992); 5: Norris (1963); 6: Carr (1994); 7: Jones (1984); 8: McCormick (1989); 9: Kanciruk & Herrnkind (1978); 10, 11: Moore & MacFarlane (1984), Skewes et al. (1997); 12: Muller (1982); 13: Phillips (1983); 14: Salman et al. (1990); 15, 16: Fry (1981), Riera et al. (2000); 17: O'Brien (1994); 18, 19, 20: Staples (1979, 1980), Vance et al. (1998); 21: Hyland et al. (1984); 22: Koenig & Coleman (1998); 23, 24, 25: Gillanders & Kingsford (1993, 1996), Gillanders (1997b); 26: Eggleston (1995); 27: Ruello (1977); 28: Benfield et al. (1990); 29: Klaoudatos et al. (1992); 30, 31: Ruello (1975), Montgomery (1990); 32: Somers & Kirkwood (1991); 33: Gunderson et al. (1990); 34, 35: Moore & Reynolds (1982), Russell & Garrett (1985); 36, 37: Allen & Herbinson (1990), Kramer (1991); 38, 39: Olson & Pratt (1973), Gunderson et al. (1990); 40: Mathews & Barker (1983); 41: Chubb et al. (1981); 42, 43: Koutsikopoulos et al. (1995), Symonds & Rogers (1995); 44: Morton et al. (1993); 45, 46: Booth (1979, 1986); 47, 48: Tabb et al. (1962), Costello & Allen (1966); 49: Hines et al. (1995); 50: Kroger & Guthrie (1973); 51: Kerstan (1991); 52: Thresher et al. (1994); 53: Blaber et al. (1999); 54: Cappo et al. (2000); 55: McCormick et al. (1998); 56, 57, 58: Royce et al. (1968), Groot & Margolis (1991), Fukuwaka & Suzuki (1998)

structure of some habitats means that each habitat often needs to be sampled using different methods (e.g. Blaber et al. 1989). In addition, using the same sampling method in all habitats would not necessarily alleviate this problem, because the efficiency of the same sampling technique used across a range of habitat types is seldom known (Eggleston & Dahlgren 2001).

Differences in the distribution of size classes among different habitats have been used frequently to infer movement from juvenile to adult habitats. However, other explanations may also account for spatially explicit patterns of organism size distribution among habitats (Table 2). For example, differences in growth rates or differential mortality among habitats may result in patterns similar to those due to movement from juvenile to adult habitats. Few studies provide estimates of mortality in juvenile habitats (but see Kramer 1991, Able 1999) and it has often been assumed that movement is of primary importance (but see Sheaves 1995, Gillanders 1997a). Knowledge of the distribution of age classes among different habitats can provide complementary information to size and provide additional evidence for movement. Only a few studies have provided this additional information (e.g. Rogers 1993, Symonds & Rogers 1995, Gillanders 1997a). As an example, spatial patterns in density and size structure of blue groper *Achoerodus viridis* (Labridae) showed that the proportion of small fish decreased from estuarine sites to open coastal reefs and that large fish showed the reverse pattern (Gillanders 1997b). Growth of *A. viridis* was then investigated to determine to what extent the differences in size-frequency distributions could be explained by slower growth at estuarine reefs compared to open coastal reefs. No significant differences in growth of *A. viridis* were found and therefore spatial differences in size-frequency distributions were most likely due to movement of fish from estuarine to coastal reefs (Gillanders 1997a).

Spatial partitioning of maturity stages was used to indicate movement from juvenile to adult habitats in 3 studies (3%; Chong et al. 1990, Eggleston 1995, Sheaves 1995). For example, Sheaves (1995) found that only immature lutjanids (*Lutjanus argentimaculatus* and *L. russelli*) and serranids (*Epinephelus coioides* and *E. malabaricus*) were found in estuaries and that these fish were much smaller and younger than fish of the same species found offshore. Similarly, early juvenile Nassau grouper *E. striatus* (30 to 120 mm total length [TL]) use macroalgal meadows in back-reef mangrove areas, and apparently migrate to nearby patch reefs (120 to 300 mm TL) and eventually offshore to adult reef (>300 mm TL) 3 to 4 yr post-settlement (Eggleston 1995). In these studies, the complete ab-

Table 2. Types of studies used to determine movement from juvenile to adult habitats, including examples

Type of study	Invertebrates	Fishes	No. of studies
(1) Distribution and abundance	Stoner et al. (1988), Stoner (1989), Vance et al. (1998)	Weinstein & Heck (1979), Kerstan (1991), Dorf & Powell (1997), Henriques & Almada (1998)	16
(2) Distribution, abundance and size structure	Gunderson et al. (1990), Salman et al. (1990), Cattrijsse et al. (1997), Skewes et al. (1997)	Blaber et al. (1989), Rooker & Dennis (1991), Bell & Worthington (1993), Gillanders (1997b)	30
(3) Size structure	Coles & Greenwood (1983), Wicker et al. (1988), O'Brien (1994), Roa et al. (1995)	Shlossman & Chittenden (1981), Griffiths (1996)	9
(4) Spatial partitioning of maturity stages	Chong et al. (1990)	Chong et al. (1990), Sheaves (1995)	3
(5) External tags (e.g. dart tags, T-bar tags)	Booth (1979), Hyland et al. (1984), Montgomery (1990), Somers & Kirkwood (1991)	Mathews & Barker (1983), Morton et al. (1993), Koutsikopoulos et al. (1995)	20
(6) Internal tags (e.g. microwire, visual implant)	Coded wire tags, van Montfrans et al. (1991)	Ferromagnetic tags, Nicholson (1978)	3
(7) Ultrasonic tags	Hines et al. (1995)	Szedlmayer & Able (1993)	5
(8) Thermal marking of otoliths	–	Urawa et al. (2000)	1
(9) Other artificial tagging methods	(e.g. marked by injection of biological stains) Costello & Allen (1966)	(e.g. freeze branding) Koenig & Coleman (1998)	2
(10) Parasites as natural tags	–	Olson & Pratt (1973)	1
(11) Stable isotopes as natural tags (e.g. $\delta^{13}C$, $\delta^{34}S$, $\delta^{15}N$)	Fry (1981), (1983), Fry et al. (1999), Riera et al. (2000)	Fry (1983)	8
(12) Micro- and trace elements as natural tags (e.g. Sr, Ba, Mn)	–	Thresher et al. (1994), Gillanders & Kingsford (1996), Yamashita et al. (2000)	3

sence of both post-juvenile size organisms in the juvenile habitat and juvenile size organisms in the adult habitat implied movement of organisms from the juvenile to adult habitats.

Artificial tags

Traditional tagging methods (e.g. external tags with internal attachments such as dart or T-bar tags) have been used primarily on diadromous species or on larger juveniles of marine fish species. Small organisms have generally not been tagged (see Table 3). Many of the studies using conventional tagging methods to determine movements of juveniles have different objectives than determining movement from juvenile to adult habitats. Some studies have reported limited movement, even for diadromous species, which would be expected to move large distances. For example, Russell & Garrett (1988) found that only 2.5% of all tagged barramundi *Lates calcarifer* were caught away from the tidal creeks in which they were tagged. Limited movement was also found for tailor/bluefish *Pomatomus saltatrix* that were tagged in Morton Bay estuary (Queensland, Australia), with no fish moving outside of Morton Bay, and all fish being recaptured within 85 km of tagging, a relatively small distance considering the wide range of the species (Morton et al. 1993). Results suggesting limited movement may be due to the fact that recapture efforts are usually concentrated near the site(s) where tagging occurred.

Internal artificial tags, such as coded wire tags (CWT) and visible implant fluorescent elastomer (VIF), have a number of advantages over more traditional tagging methods (see Table 3 for advantages). Many hatchery-reared salmonids are tagged with CWT on release in rivers, enabling their origins to be determined when they are recaptured as either juveniles or adults at sea (Courtney et al. 2000). We are not aware of any studies that have used VIF tags to track movement of organisms from juvenile to adult habitats. Most studies using VIF tags have monitored juvenile fish over only a few months (e.g. Beukers et al. 1995, Frederick 1997a,b) or focused on larger freshwater fishes (Bonneau et al. 1995, Dewey & Zigler 1996). Since juvenile invertebrates and fishes may spend many months in juvenile habitats before moving to adult habitats, the feasibility of using these sorts of tags may

Table 3. Summary of tagging methods and their advantages and disadvantages. The references provide useful papers on the tagging methods as well as examples of papers that have used the methods for determining movement from juvenile to adult habitats

Tagging method	Description of method	Advantages	Disadvantages	Source
Artificial tags				
Traditional tags (e.g. dart or T-bar tags etc.)	External tags with internal attachments	Individuals can be recognised	Tags frequently too large in proportion to size of juvenile organisms; high rates of natural juvenile mortality, low rates of recapture of tagged fish, large numbers of animals need to be tagged to produce low numbers of recaptures (applicable to all artificial tagging methods)	Russell & Garrett (1988), Morton et al. (1993)
Internal tags (e.g. coded wire tags, visible implant fluorescent [VIF] tags)	Internal tag with no external attachment;VIF tags administered as subcutaneous liquid injection which later hardens and is visible through skin	Small fish (e.g. 8–11 mm SL) can be tagged; relatively long retention times (several months to a year); few biological side effects; individuals can be recognised	Most suitable for hatchery-reared fish (e.g. salmonids), visibility of tags over long time periods (years) unknown	Buckley et al. (1994), Beukers et al. (1995), Frederick (1997b), Courtney et al. (2000)
Telemetry techniques	Track and determine the location of individuals in real time, transmits data *in situ* by satellite links, underwater acoustic modem or radio, or stores information for subsequent retrieval	Tags can store information until organism recaptured as part of fishery; individuals can be recognised	Need to continuously track organisms; may be problems where organisms move large distances, into very deep water or under adverse sea conditions; tags need to be less than 2% of body weight of organism	Szedlmayer & Able (1993), Wolcott (1995), Freire & Gonzalez-Gurriaran (1998), Kraus (1998), Sibert & Nielson (2001)
Compounds incorporated into calcified tissues (e.g. fluorescent chemicals, trace and micro-elements, radioactive isotopes)	Artificial marks that batch-tag organisms; organisms are usually immersed in solution containing compound	Able to tag many organisms relatively quickly	Uncertain whether such compounds produce good, long-term marks; determining whether adult individuals are tagged may be time consuming in terms of preparation and analysis of samples	Ennevor & Beames (1993), Jones et al. (1999)
Temperature fluctuations	Mass marking method that uses short-term temperature fluctuations to change appearance of discontinuous and incremental zones in one or more increments of the otolith	Can identify groups of fish using Morse code, the bar code or RBr system but not usually individuals	Most suitable for hatchery-reared fish (e.g. salmonids) and difficult to mass-mark large numbers of wild fish; time consuming to prepare and read otolith samples of adults; costs of changing temperature may be prohibitive	Volk et al. (1999), Urawa et al. (2000)
Natural tags				
Individual marks	Individuals can be distinguished by differences in markings	Individuals can be recognised; can follow individuals over time	May not be suitable for many species	Grimes et al. (1986), Connell & Jones (1991)
Natural parasites	Target organism should become infected with a parasite only when they occur in the endemic area of the parasite. If infected fish is found outside the endemic area of the parasite, then it can be inferred that the fish has moved from that area	No handling of juvenile fish required (also applicable to stable isotopes and elemental signatures)	Parasite needs to infect young fish in juvenile habitat and adult should not be susceptible to further infection; parasitic infection needs to be maintained for a sufficient period to be found in fish in adult habitat	Olson & Pratt (1973), Williams et al. (1992), MacKenzie & Abaunza (1998)
Stable isotopes	Isotopic signature of tissues will reflect the assimilated diet or environmental conditions integrated over the time period equal to the turnover of the tissue measured	All organisms are essentially 'tagged' so all adults represent a recapture (also applicable to elemental signatures)	Relies on difference in isotopic signatures between different areas; turnover time of signature in tissue may be too quick to track movement of some organisms	Fry (1981), Fry et al. (1999), Hobson (1999), Kennedy et al. (2000),Weber et al. (2002)
Elemental signatures	Elemental signature incorporated into calcified tissues as organism grows; differences in signatures between different areas/habitats allow fish to be recognised	Able to relate differences to age of organism	Relies on differences in elemental signature between different areas; signature must be stable over time; assumes that signatures are known for all source habitats	Thresher et al. (1994), Gillanders & Kingsford (1996), Campana (1999), Yamashita et al. (2000)

depend on the visibility of the tags over longer time periods. Juvenile organisms grow fairly rapidly and therefore it is possible that growth of surrounding tissue may limit visibility of tags.

Telemetry techniques, which track and determine the location of individuals in 'real-time', show great promise as a method to determine links between juvenile and adult habitats. Szedlmayer & Able (1993) used ultrasonic transmitters to estimate residence time and movements of juvenile summer flounder *Paralichthys dentatus* in a subtidal creek. All tagged fish eventually moved out of the creek and it was suggested that this was part of a seasonal migration to the adult habitat. With continued miniaturisation of electronic components and micropower transducers, telemetry may offer a viable alternative to other artificial tagging methods for very small organisms (Sibert & Nielson 2001). This may be especially likely with archival (e.g. West & Stevens 2001) and pop-up tags (e.g. Block et al. 1998).

Although many of the tagging methods mentioned above allow individuals to be recognized, this may not be necessary in detecting movement from juvenile to adult habitats. Compounds that are incorporated into calcified tissues, such as fluorescent chemicals (e.g. alizarin complexone, calcein, tetracycline), trace- and micro-elements (e.g. rare earth elements, strontium) and radioactive isotopes, may be applied as artificial marks to batch tag organisms (e.g. Ennevor & Beames 1993, Jones et al. 1999). We are not aware of any studies that have used these methods to determine movement from juvenile to adult habitats, although Jones et al. (1999) successfully used tetracycline to mark otoliths of developing embryos of a coral reef fish (*Pomacentrus amboinensis*) to determine whether or not populations were self-recruiting.

Temperature fluctuations have also been used to induce patterns onto otoliths as a means of mass-marking (Table 3, Volk et al. 1999). The geographic origins of chum salmon from the high seas have been determined using thermal marks in otoliths (Urawa et al. 2000).

Natural tags

In an effort to overcome some problems with artificial tagging methods, alternative techniques such as natural tags have been investigated. In some instances individual marks have been used to identify marine mammals and turtles. There are a few studies that have used this approach for fishes (e.g. Grimes et al. 1986, Connell & Jones 1991). In 12% of the studies reviewed, parasites, trace elements, and stable isotopes have been used as natural tags to determine movement from juvenile to adult habitats (e.g. Fry 1981, 1983, Thresher et al. 1994, Gillanders & Kingsford 1996, Fry et al. 1999, Riera et al. 2000).

Natural parasites have been used as biological tags (e.g. Olson & Pratt 1973) to detect movement from estuary to adult habitat. Olson & Pratt (1973) found that certain parasites (e.g. the acanthocephalan, *Echinorhynchus lageniformis*) were acquired by English sole *Pleuronectes vetulus* only while in the estuary and not whilst offshore. The incidence of infection in estuarine fish before emigration was similar to the incidence in 0-group fish collected offshore after emigration, suggesting that there was little or no influx of young from potential non-estuarine habitats (Olson & Pratt 1973).

Stable isotopes can be used to trace the origin or movement of organisms because isotopic signatures in animal tissues reflect those of local food webs or of the aquatic habitat in which they have grown (Table 3). Isotopic signatures of food webs or water masses vary spatially depending on biogeochemical processes (Hobson 1999, Kennedy et al. 2000). The contribution of diet versus water to the isotopic signal is likely to depend on the isotope. Several studies have used a variety of stable isotopes (e.g. $\delta^{13}C$, $\delta^{15}N$, $\delta^{34}S$) to investigate movement, including Fry (1981), who examined $\delta^{13}C$ values in tissues of brown shrimp *Penaeus aztecus* as they moved from inshore seagrass beds to offshore areas. Offshore habitats with a phytoplankton-based food web are depleted in ^{13}C relative to a seagrass-based food web. Sub-adult individuals collected offshore had $\delta^{13}C$ values typical of individuals in seagrass meadows, suggesting that they had moved from seagrass to offshore regions (Fry 1981).

Elemental signatures (e.g. Sr, Mn, Ba) in otoliths of fish have also been used to evaluate links between juvenile areas and adult stocks (e.g. Thresher et al. 1994, Gillanders & Kingsford 1996). The acellular and metabolically inert nature of otoliths means that many of the elements that are used as a natural tag and accreted onto the growing surface of the otolith are permanently retained (Campana 1999). The otolith continues to grow through time, ensuring that the entire lifetime of the fish has been recorded and differences in chemistry between layers can be resolved to within days or years of their deposition. The calcium carbonate and trace elements that make up 90% of the otolith are derived primarily from the water (Milton & Chenery 2001), although there are likely to be physiological filters that prevent a simple linear relationship between the concentration of elements in the water and the otolith (Campana 1999). Analysis of either whole otoliths or small areas within the otolith have been used to distinguish stocks or sub-populations of marine species (e.g. Edmonds et al. 1989, 1991, 1992, Campana et al. 1994, Campana & Gagne 1995, Proctor et al. 1995), to reconstruct the history of water temperatures experienced by a fish throughout its life (e.g. Patterson et al. 1993), to detect anadromy (e.g. Kalish 1990, Secor 1992, Coutant & Chen 1993) and to determine connectivity between populations (e.g. Gillanders & Kingsford 1996, DiBacco & Levin 2000, Yamashita et al. 2000, Thorrold et al. 2001, Gillanders 2002).

Two different approaches have been used to determine geographic origins of fish using elemental chemistry of otoliths. Gillanders & Kingsford (1996) found significant differences in the elemental signatures of otoliths of juvenile blue groper *Achoerodus viridis* collected from 2 habitats: seagrass and rocky reef. The central region of adult otoliths corresponding to that laid down when the fish was a juvenile was then analysed to determine the relative importance of the 2 juvenile habitats in supporting adult stocks and to demonstrate links between juvenile and adult habitats. Conversely, Thresher et al. (1994) assessed the otolith composition at the primordium—an area corresponding to a spawning ground tag—of adult jackass morwong *Nemadactylus macropterus*. The samples were suggested to group into 3 offshore breeding populations. Juveniles were then collected from 2 known 'nursery' grounds and the composition of their primordial region analysed. The data from adults were then used to classify each juvenile and calculate the probability that it originated in each of the 3 breeding populations (Thresher et al. 1994).

Results from several studies indicate that juveniles from individual estuaries can be distinguished using elemental signatures (Thorrold et al. 1998, de Pontual et al. 2000, Gillanders & Kingsford 2000), thereby suggesting that the recruitment and/or natal origins of adult fish can be determined (see Gillanders 2002). Thorrold et al. (2001) used elemental and stable isotope signatures in otoliths of weakfish *Cynoscion regalis* to determine natal sources and found that 60 to 81% of fish returned to natal estuaries for spawning. Swearer et al. (1999) have also used otolith chemistry to reconstruct the dispersal history of recruiting larvae. These studies demonstrate that there is much promise in using geochemical signatures to determine population connectivity such as links between juvenile and adult habitats.

Spatial and temporal scales of movement

The scale of movement from juvenile to adult habitat ranged from movements over metres (e.g. queen conch *Strombus gigas*, Stoner et al. 1988, Stoner 1989) to movements over thousands of kilometres (e.g. Australian salmon *Arripis truttaceus*; Cappo et al. 2000) (Table 1). The majority of fish and crustaceans, however, moved distances of kilometres to hundreds of kilometres from juvenile to adult habitats (Fig. 2, Table 1). Some organisms moved a range of scales depending on the study. For example, eastern king prawns *Penaeus plebejus* moved tens of kilometres in one study (Ruello 1975), but up to hundreds of kilometres in another (Montgomery 1990).

The duration of time spent in juvenile habitats ranged from days to years, but averaged 13 mo (±2 mo; n = 67). For example, juvenile blue crabs *Callinectes sapidus* spent as few as 8 d (but up to 65 d) in tidal marsh creeks before moving to sub-adult and adult habitats (van Montfrans et al. 1991). Similarly, adult Caribbean spiny lobster *Panulirus argus* move back and forth on a seasonal basis between offshore adult reef habitats where mating occurs, and inshore shallow foraging grounds during summer and fall (Lipcius & Eggleston 2000). By comparison, yellowtail rockfish *Sebastes flavidus* and rock lobster *Panulirus cygnus* could spend up to 5 yr in the juvenile habitat (Mathews & Barker 1983, Phillips 1983).

Although a number of studies have shown connectivity between juvenile and adult habitats, very few have determined the relative contribution of different juvenile habitats to the adult population (e.g. Gillanders & Kingsford 1996, Yamashita et al. 2000, Gillanders 2002). Using Sr:Ca ratios, Yamashita et al. (2000) showed that 65 and 32% of the adult stone flounder *Platichthys bicoloratus* population were produced from

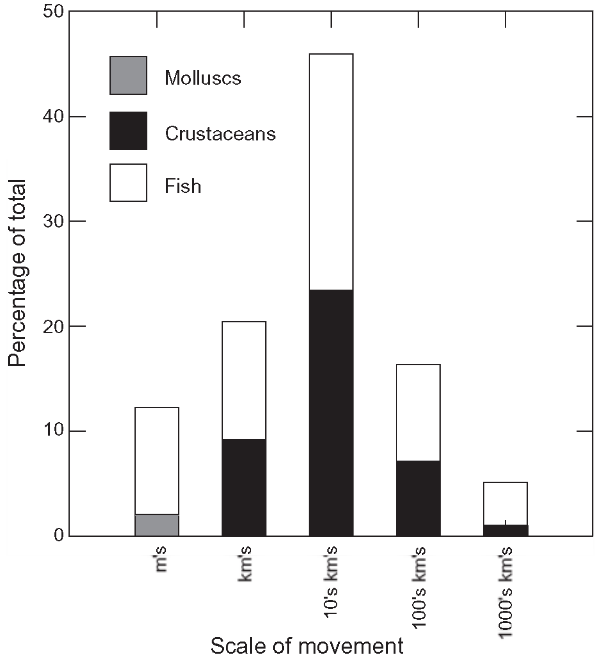

Fig. 2. Frequency histogram showing scale of movements from juvenile to adult habitats for molluscs, crustaceans and fishes (n = 98). The scale of movement was only indicated in some of the studies examined

estuarine nursery areas in 1994 and 1995, respectively. The estuarine nursery grounds made up only 6 % of the total nursery grounds, but juvenile density was 5 to 50 times higher in estuaries than in exposed offshore waters, indicating that estuaries are important nursery grounds (Yamashita et al. 2000). These results suggest that the relative contribution of different habitats may vary over time (e.g. among years). The contribution of different habitats or estuaries to the adult population may also vary between different regions.

Management implications

Overall, there were few studies (Table 4) that demonstrated good evidence for movement from juvenile to adult habitats. A large part of this may be due to the fact that little of the research was aimed at directly answering questions relating to this type of movement (e.g. Bell & Worthington 1993). In addition, many studies focused either on the juvenile or adult stage of the life history, rather than on both stages. For example, many studies have sampled juvenile habitats and assumed that once organisms are no longer found there, they have moved to adult habitats. While this may be the case, it does not provide strong evidence that organisms have successfully moved to adult habitats or which juvenile habitats may contribute the most individuals to the adult population. Further, sampling was often limited to one type of habitat or to one location within each type of habitat, which restricts the conclusions that may be drawn. There is a clear need to obtain information on abundance and size distribution of organisms from a range of juvenile and adult habitats, and to sample at multiple locations within each type of habitat.

Although direct tagging is in theory the most effective method for showing movements between juvenile and adult habitats, there are problems when dealing with large numbers of wild fish that need to be tagged at a small size (see Table 3). The evidence is strongest for penaeid prawns, where individuals that were tagged in estuaries have been recaptured offshore (Ruello 1975, 1977, Montgomery 1990). Ruello (1977) found recapture rates from 0 to 7.7 %, depending on the estuary in which the prawns were released, suggesting that large numbers need to be tagged to make strong inferences regarding habitat linkages. Studies on fish have generally focused on tagging larger juveniles rather than smaller, newly recruited individuals.

Table 4. Studies that show good evidence of movement between juvenile and adult habitats. Spatial and temporal scales of movement between juvenile and adult habitats, and method used to determine movement is shown

Organism	Spatial scale	Temporal scale	Method	Source
Queen conch *Strombus gigas*	Tens of metres	1–3 yr	Distribution and abundance, tagging and direct observations	Stoner et al. (1988), Stoner (1989)
Brown shrimp *Penaeus aztecus*	Kilometres to tens of kilometres	<3 mo	Stable isotopes ($\delta^{13}C$)	Fry (1981)
Pink shrimp *Farfantepenaeus duorarum*	Tens of kilometres	<6 mo	Stable isotopes ($\delta^{13}C$ and $\delta^{15}N$)	Fry et al. (1999)
Pink shrimp *Farfantepenaeus duorarum*	Not indicated	Not indicated	Mark-recovery experiments with biological stains	Costello & Allen (1966)
Eastern king prawns *Penaeus plebejus*	Less than 100 km from juvenile to adult habitats, but up to 1000 km to reproductive habitat	Not indicated	Atkins-type tags (external tag)	Ruello (1975, 1977)
Eastern king prawns *Penaeus plebejus*	10–160 km, but up to 1200 km to spawning grounds	<3–4 mo	Streamer tags (external tag)	Montgomery (1990)
Sole *Solea solea*	40–80 km	<2 yr	Petersen disc attached with a titanium wire just in front of pectoral fin (external tag)	Koutsikopoulos et al. (1995)
Atlantic menhaden *Brevoortia tyrannus*	Kilometres to hundreds of kilometres	<1 yr	Numbered ferromagnetic tag (7.0 × 2.5 × 0.4 mm)	Kroger & Guthrie (1973)
English sole *Pleuronectes vetulus*	Tens of kilometres	<1 yr	Natural parasites	Olson & Pratt (1973)
Blue groper *Achoerodus viridis*	Kilometres to tens of kilometres	3–4 mo	Elemental signatures (Mn, Sr and Ba in otoliths)	Gillanders & Kingsford (1996)
Stone flounder *Platichthys bicoloratus*	Tens of kilometres	<1 yr	Elemental signatures (Sr:Ca ratios in otoliths)	Yamashita et al. (2000)
Snapper *Pagrus auratus*	Kilometres to tens of kilometres	<2 yr	Elemental signatures (Mg, Mn, Sr and Ba in otoliths)	Gillanders (2002)

In the future, further evidence for movement from juvenile to adult habitats is likely to come from mark-recapture methods using artificial tags, especially as the size of tags continues to decrease. Natural tags, such as stable isotopes and trace elements, also show great potential for determining movement from juvenile to adult habitats and are currently providing the best results (e.g. Fry 1981, Gillanders & Kingsford 1996). Future research needs to focus on the temporal stability of such signatures and the spatial scale over which differences in signatures are found, as few studies currently address these issues.

As human activities continue to eliminate or fragment habitats, an understanding of connectivity between juvenile and adult populations becomes increasingly important. Connectivity is likely to depend not only on the distance between the 2 habitats, but also on the presence of movement corridors or stepping-stones of natural habitat. Failure to protect habitats and the capacity of fish to move freely among them may have detrimental effects on adult populations. For example, if organisms only move from juvenile to adult habitats along vegetated corridors, and do not move over unvegetated habitats, then factors contributing to degradation of vegetated habitats may also contribute to a decline of the adult populations that rely on these juvenile habitats as sources of recruits. Telemetry techniques may be most appropriate for addressing questions related to movement along corridors.

Knowledge of connectivity between juvenile and adult populations and determination of potential habitats that supply more recruits to adult populations (e.g. Fig. 4 in Beck et al. 2001) have considerable implications for fisheries management and the effective conservation of organisms. If some habitats or sites (e.g. estuaries) show strong links to adult populations, and these sites contribute to replenishing adult populations, then such sites may indicate source areas and should potentially be set aside as marine protected areas. Efforts in management and habitat conservation could also be more judiciously invested in particular sites rather than focusing on all seagrass, marsh or mangrove habitats.

It is critical to measure movement of individuals if we are to understand better the role of so-called nursery habitats in the life cycle of marine organisms. Movement must be monitored from all types of habitat in which the juvenile is found, because the nursery role hypothesis focuses on the different types of habitat utilised by juveniles, and not just a selected subset of habitats (Beck et al. 2001). Determining which juvenile habitats contribute more per unit area to the production of individuals that recruit to adult populations will allow management and conservation efforts to focus on those habitats that make the greatest contribution to adult populations.

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