



# A re-examination of fish estuarine dependence: Evidence for connectivity between estuarine and ocean habitats

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## Abstract

Our understanding of the recruitment of estuarine fishes has been strongly influenced by two views: first, that estuaries are important nurseries and second, that many species are estuarine dependent. Based on an attempt to review the world-wide literature on these topics, it appears that both of these views have merit but could benefit from additional attention and clarification. The term estuarine dependency is used in a variety of ways depending on the author and context and even how one defines estuary. Further, and perhaps most importantly, we often lack the comparative data on habitat use by fishes in the ocean vs. the estuary to make judgments about dependency. To that end we have analyzed the distribution patterns of fish species along the estuarine-coastal ocean ecotone in southern New Jersey, U.S. to evaluate the fish response. As a result, it appears the degree of estuarine use is quite variable among species, as well as at geographic, annual and cohort-specific scales. Thus, further synthesis is necessary and it might focus on: first, more information on fish use in different types of estuaries across a broad geographical range; second, a better understanding of the functional significance of habitats across the habitat landscapes of the estuary–ocean ecotone; third, any further synthesis needs to incorporate the role of biotic variables (e.g. predation, competition) in order to enhance our understanding of the degree of estuarine dependency; fourth, we need to determine how freshwater flow into estuaries might influence habitat use especially with regard to the potential role of the offshore estuary.

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## 1. Introduction

Estuaries are the focus of attention because of the concentration of large components of the human population in these watersheds (Alongi, 1998; Lindeboom, 2002), the resulting increasing urbanization of coastal watersheds (Valiela et al., 1990, 1992) and concomitantly the alteration and loss of habitats, as in the U.S. (National Research Council, 1994; Simenstad et al., 2000). In addition, the economic value for “estuarine dependent” fish species is well documented in the U.S. (McHugh, 1985; Houde and Rutherford, 1993;

Chambers, 1992), and Gulf of Mexico (Lindall and Saloman, 1977; Yáñez-Arancibia et al., 1985), Australia (Newell and Barber, 1975; Pollard, 1981; Lenanton and Potter, 1987), Africa (Blaber, 2000), and South America (Castello, 1985). Much of this economic value is based on the high productivity that typically occurs in these systems (Allen, 1982; Deegan and Thompson, 1985).

As a result of this importance, during the last decade there has been an increasing research emphasis on fish habitats (Benaka, 1999) and simultaneously an increased focus on legislation, in the U.S., including the long-term protection of Essential Fish Habitat (Baird, 1999; Schmitten, 1999). While this recognition of the importance of fish habitat seems recent, it has actually developed over the last half century with origins in an

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early understanding of “nurseries” and “estuarine dependence.” Unfortunately, until recently, these terms were undefined and used very liberally, and not consistently. Also, we lack a synthesis of these and other habitat landscapes (Hobbie, 2000; Boesch et al., 2000).

The purpose of this paper is to specifically re-examine the limits and use of the terms “nurseries” and “estuarine dependence,” especially as they relate to fish habitat connectivity between estuaries and the coastal ocean. The expectation is that it is not possible to completely define these terms to everyone’s satisfaction because of several inherent difficulties associated with the life history and behavior of fishes. First, fishes have complex life histories and habitat use may vary widely among life history stages (Kendall et al., 1984; Whitfield, 1990; Able and Fahay, 1998). Additionally, the life histories of many species are poorly known, even for those of economic importance. Second, the behavior of fishes is inadequately understood, especially as many forms, and especially those of economic importance, are highly migratory. Third, many areas of the estuary-coastal ocean ecotone are poorly or inconsistently sampled and seldom sampled synoptically. This shortcoming is best expressed in the reminder that we have to know about patterns before we can understand processes (Underwood et al., 2000). Fourth, the patterns of fish use of estuaries are complicated, and attempts to classify these patterns vary in their focus and applicability. Some of these classifications are based on reproduction (e.g. Dando, 1984; Whitfield, 1994, 1998), timing of spawning and entrance into the estuary (e.g. Deegan and Thompson, 1985; Able and Fahay, 1998), response to salinity (Bulger et al., 1993) and life histories (Haedrich, 1983; Whitfield, 1994). These attempts to organize or classify estuarine fishes are compounded for temperate fishes that leave estuaries in winter (e.g. Able and Fahay, 1998) or as they increase in size or reach some size threshold (see citations in Potter et al., 1997; Rountree and Able, 1992). Fifth, the treatment of the seaward limits of estuaries varies among authors and thus confounds the concept of estuarine dependency (see below).

## 2. Historical development of our understanding

The most focused attempt to understand fish use of estuaries, that we are aware of, began in the Gulf of Mexico with the observation that “The young of many animals usually thought of as marine, require areas of low salinity for nursery grounds” (Günter, 1945, 1950; Pearse and Günter, 1957). Subsequently, the “marine–estuarine life history” was considered a general law for many species of fishes (Günter, 1967). Others have referred to fishes with this life history as “marine

transients” (Deegan et al., 2000) or estuarine-catatromy (Bulger et al., 1995; Lowery et al., 1995). At the same time, several authors did not define the term but provided a list of “estuarine dependent” species for the Gulf of Mexico and east coast of the U.S. (McHugh, 1967; Clark, 1967) and an expanded list for all coasts of the U.S. (Stroud, 1971). Subsequently, Darnell and Soniat (1979), while working in the Gulf of Mexico, noted the difference between “estuarine related” i.e., coastal marine forms which inhabit the estuary with some regularity but which do not require this habitat and “estuarine dependent” i.e., species which usually require the estuarine habitat for some stage of the life history. A somewhat different interpretation, as developed from observations in South Africa, Australia, and England is that “estuarine opportunists” or “marine estuarine opportunists” are those species that typically inhabit both estuaries and inshore marine environments (Lenanton and Potter, 1987; Potter et al., 1997). Other evaluations of estuarine dependency in South Africa and Australia suggested that only those taxa whose populations would be adversely affected by the loss of estuarine habitats should be considered estuarine dependent (Blaber et al., 1989; Whitfield et al., 1994).

Other observers have questioned the general applicability of fish “estuarine dependence” because the focus has been on sampling estuaries for fishes while there has been little effort on the adjacent inner continental shelf in both temperate (Able and Fahay, 1998; Martino and Able, 2003) and tropical (Longhurst and Pauly, 1987; Blaber, 2000) systems. Thus, the admonishment by Günter (1956) that there are few studies examining species along the gradient between tidal freshwater of estuaries and the coastal ocean may still be applicable, to some degree. Exceptions to this are evident from Australia (Lenanton, 1982; Blaber et al., 1989, 1995), South Africa (Lasiak, 1986; Bennett, 1989; Valesini et al., 1997; Harris et al., 2001; Strydom, 2003), and Mexico (Yáñez-Arancibia et al., 1985).

The development of ideas revolving around the concept of estuarine dependence are often related to our understanding of “nurseries.” In fact, the first use of the term nursery grounds that we have found is part of the description of estuarine dependence (Günter, 1945; Pearse and Günter, 1957). Thus, the terms have had long, sometimes parallel usage, largely because early researchers considered the entire estuary to be a nursery. More recently there has been more emphasis on individual habitats such as salt marshes (Minello et al., 2003), seagrasses (Heck et al., 2003) and mangroves (Sheridan and Hays, 2003). Fortunately, a recent review of the nursery concept (Beck et al., 2001, 2003) has clarified our understanding by defining nurseries as the habitats of the juveniles of a species that contribute more, on average, to the production of individuals to the

adult population, than other habitats in which the juveniles occur. This definition, thus, makes a clear distinction between juvenile and nursery habitats, something many recent authors have not done. This lack of differentiation accounts for the frequent use of “nursery” in the literature without any understanding of how a particular habitat may contribute relative to other habitats, i.e. the functional significance of each habitat type. Further, the revised definition of nursery is based on four comparative factors: (1) density, (2) growth, (3) survival, and (4) movement to adult habitats, i.e. contribution to the adult populations (Beck et al., 2001, 2003). Frequently only one of these factors may be evaluated (most frequently density, Minello et al., 2003; Heck et al., 2003) but all are necessary for the identification of nurseries, including the movement to adult habitats, which is probably the least frequently studied (Gillanders, 2002; Gillanders et al., 2003). These criteria/approaches, in turn, are critical to accurately resolve the degree of estuarine dependence and should be part of future evaluations. A related term “Essential Fish Habitat” is defined as those waters and substrate necessary for spawning, breeding, feeding or growth to maturity (Baird, 1999). This definition and its determination is the current focus, by law, of all managed species in the U.S. (NOAA, 1996; Benaka, 1999; Schmitten, 1999), and is being applied to non-commercial species as well (e.g. Able, 1999; Able and Hagan, 2003).

### 3. Definition of estuary

An important clarification that needs to be made is how to define estuary in order for the term estuarine dependence to have any relevance. Admittedly, this is a complex issue that has been frequently revisited since the earliest attempts to study estuaries in a comprehensive fashion (Cameron and Pritchard, 1963; Lauff, 1967; Hedgepeth, 1967; Day, 1981; Elliott and McLusky, 2002). Although the following are not exhaustive, they do represent the spectrum (geomorphology, hydrography, sediments, fauna) of definitions found in the literature. Odum (1959) described an estuary as a “river mouth where tidal action brings about a mixing of salt and fresh water,” whereas Pritchard (1967) defines it as “a semi-enclosed body of water which has a free connection with the open sea and within which sea water is measurably diluted with fresh water derived from land drainage.” Others have noted the similarities between lagoons and estuaries and defined “lagoon–estuarine environments” as “shallow, semi-enclosed water bodies of variable volume, connected to the sea in a permanent or ephemeral manner, with variable temperature and salinities, permanent muddy bottoms, high turbidity, irregular topographic characteristics, and

biotic elements” (Yáñez-Arancibia et al., 1994). This definition is also sufficiently broad that it includes hypersaline estuaries/lagoons (Cowardin et al., 1997), and also estuaries with ephemeral connections to the ocean (Lenanton and Hodgkin, 1985; Whitfield, 1998). These and many other definitions share a geomorphological component and are often based on a “semi-enclosed body of water.” McHugh (1967) has taken a different approach and defined the nektonic estuary as “including inshore and offshore (i.e. <33.5 salinity) components.” This extends the estuary into continental shelf waters (Cameron and Pritchard, 1963) and broadens the spatial scale of the definition, but he offers little explanation for the salinity boundary proposed. The offshore estuary may overlap with the shoreface entrainment volume of Ray (1991) and Ray and Hayden (1992). This same broader view is consistent with the term “estuarine zone,” i.e. “an environmental system consisting of the estuary and those transitional areas consistently influenced or affected by water from the estuary” (Smith, 1966). Others have argued, from a geological perspective, that estuaries are short-lived environments (Russell, 1967; Schubel and Hirschberg, 1978; Haedrich, 1983; Whitfield, 1994; Attrill et al., 2001); however, it is reasonable to assume that estuaries have existed at the land-sea interface for long periods of time (e.g. Deegan and Thompson, 1985), thus the background for the evolution of “estuarine dependent” or “estuarine opportunist” life styles (Blaber et al., 1989).

### 4. Current understanding

There is certainly ample evidence, from around the world, that juvenile fishes use estuaries, regardless of the above definition one chooses. (Throughout the rest of this paper the definition of estuary follows that of Pritchard, 1967.) The evidence for estuaries as juvenile habitat is best documented from South Africa (e.g. Whitfield, 1998), Australia (e.g. Potter et al., 1990; Blaber, 2000), and the U.S. (e.g. McHugh, 1967; Ray, 1997; Ray et al., 1997; Able and Fahay, 1998) based primarily on the abundant estuaries in each of these countries and the resulting long focus of researchers and managers. Other documentation of the importance of estuaries is available from temperate South America (Chao et al., 1982), tropical estuaries in the Philippines, Mexico and elsewhere (Yáñez-Arancibia, 1985; Longhurst and Pauly, 1987; Blaber, 2000), and more recently Europe (Elliott and Hemingway, 2002).

In many instances the patterns of fish use of semi-enclosed estuaries are similar across the world. The categories of fish life cycles associated with South African estuaries (i.e. Whitfield, 1998, slightly modified) can be found in estuaries in all of the other continents

of the world. These include the following categories: (Ia) estuarine species that breed only in estuaries, (Ib) estuarine species that breed in estuaries and the marine environment, (IIa) euryhaline marine species that usually breed in the ocean but the juveniles are dependent on estuaries as nursery areas, (IIb) euryhaline marine species that usually breed in the ocean, with the juveniles occurring in estuaries but also being found in the ocean, (IIc) euryhaline marine species that usually breed in the ocean, with the juveniles occurring in estuaries but being more abundant in the ocean, (III) marine stragglers not dependent on estuaries, and (IV) diadromous species. These can be grouped into obligate and facultative users, a point frequently made in the literature from diverse sources and locations (e.g. Blaber, 2000).

While there are consistencies in the patterns of the life cycles of many estuarine fishes, there are multiple sources of variation in how, and the frequency with which, fishes use estuaries; these vary with physical and biological factors. In many instances, geomorphology influences estuarine use such as along the east coast of the U.S. where the low-lying coastal plain has allowed the formation of many large, permanent estuaries (McHugh, 1967), whereas in South Africa many estuaries are seasonally or annually closed (Potter et al., 1990; Whitfield, 1998). The latter may account for the frequency of “estuarine opportunists” in areas of Australia (Lenanton and Potter, 1987). In these instances other habitats, such as ocean waters, must supply alternative habitat. However, it is important to determine if these alternative habitats provide the same habitat quality. In some studies, reported growth rates of some species are greater in the estuary than in marine waters (Lenanton and Potter, 1987; Le Pape et al., 2003; Yamashita et al., 2003). Other broad-scale differences in fish use of estuaries may vary between tropical and temperate estuaries. For example, it has been suggested that, in tropical waters, the inner continental shelf is used by fishes as a juvenile habitat in much the same way as estuaries (Blaber and Blaber, 1980; Blaber, 1981; Longhurst and Pauly, 1987). This “estuarization” of the continental shelf is due to the extension of some estuarine conditions, e.g. low salinities and muddy deposits, onto the shelf as occurs off Guiana (Lowe-McConnell, 1962) and in the Gulf of Carpentaria (Ranier, 1984; Blaber et al., 1989). This blurring of any distinction between the fish faunas of the estuary and the ocean in the tropics may be increased as the result of penetration of the ocean by estuarine species during the monsoon season (Longhurst and Pauly, 1987). Another possibility is that “estuarization” may be more widespread than just the tropics but could occur wherever large amounts of freshwater impinge on the continental shelf, thus allowing typically estuarine species to occur there. The

“estuarization” of the continental shelf is similar to the “offshore estuary” of McHugh (1967) which is also consistent with observations on the inner shelf off southern New Jersey (Milstein, 1981) and in the Gulf of Mexico (Chittenden and McEachran, 1976; Yáñez-Arancibia et al., 1985). Alternatively, reduced freshwater flow, either seasonally or consistently over time, may allow typical continental shelf species to occur in the lower portions of estuaries (see below). Other physical factors that may allow the use of alternative habitats in the ocean are physical protection and reduced wave action (in some areas), turbidity (Blaber and Blaber, 1980), and freshwater input (Strydom et al., 2002).

The use of estuaries may also vary over long temporal scales, especially when associated with climate change (Attrill and Power, 2002). As an example, it is apparent that *Micropogonias undulatus* has expanded its use of estuaries in the central portion of the Middle Atlantic Bight off the east coast of the U.S. in association with a general warming trend over the last decade.

Biological sources of variation also contribute to patterns of estuarine use by fishes, including the reduced cost of osmoregulation (Potter et al., 1990). Although it is convenient to ascribe increased food and decreased predation as advantages of estuaries (Boesch and Turner, 1984; Yáñez-Arancibia et al., 1980; Blaber and Blaber, 1980), the comparative data for oceans vs. estuaries to support or reject these ideas are basically unavailable. Some biotic sources of variation may also be responsible for the differences in estuarine and ocean use patterns. For example, we have yet to understand how annual variation in fish abundance affects estuarine vs. ocean use (e.g. Horn and Allen, 1985), or why different spawning cohorts have different patterns of estuarine vs. ocean use (e.g. Neuman and Able, 2003). Further, the possibility that different contingents exist within the same population within a single estuary, e.g. *Morone saxatilis* (Secor, 1999; Secor et al., 2001), can influence timing and duration of estuarine vs. ocean use.

## 5. Recent re-examinations

In an attempt to further evaluate the degree of connectivity between estuarine and ocean habitats, we determined patterns of habitat use for young-of-the-year fishes in southern New Jersey, U.S. (Fig. 1, see Kennish, 2004 for a fuller description of this estuary) over a number of years with a variety of sampling gears. Briefly, the study area is an estuarine to inner continental shelf corridor in southern New Jersey. The estuarine portion of this corridor is polyhaline and shallow (salinity range 21–28, Kennish and O'Donnell, 2002; average depth at mean low water is 1.7 m; Durand, 1984), with a wide annual temperature range



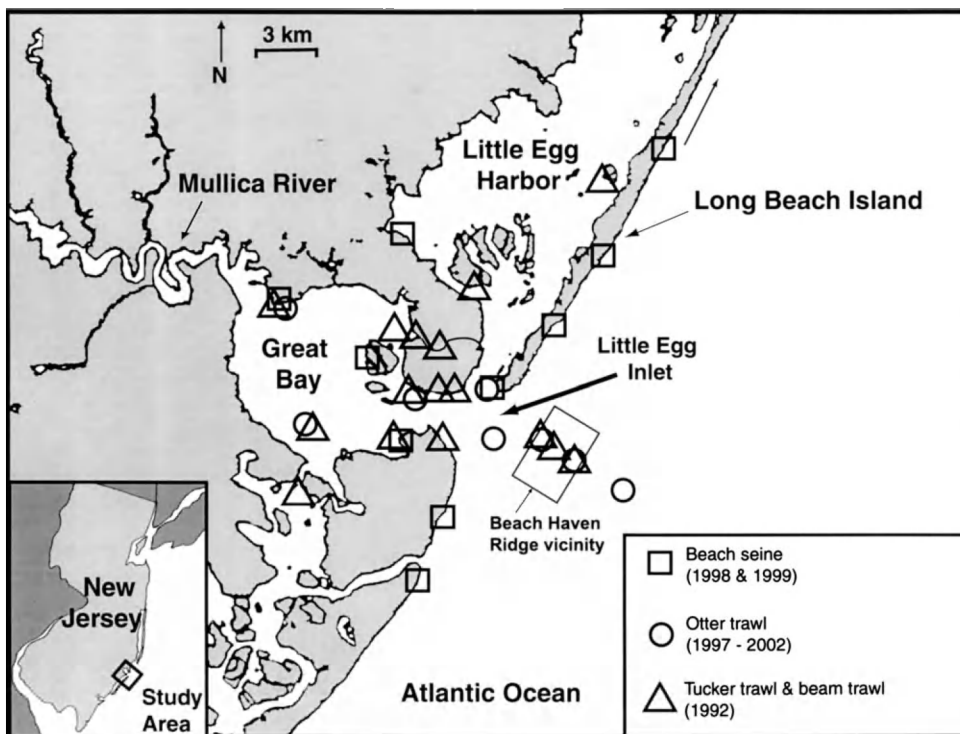


Fig. 1. Study area across the Great Bay-Little Egg Harbor estuary-ocean ecotone in southern New Jersey, U.S. based on Martino and Able (2003) and unpublished data. Several other ocean beach seine stations on Long Beach Island were located further north of the arrow.

( $-2$ – $28$  °C; Able et al., 1992), a moderate tidal range (1.1 m near the mouth of Great Bay; Durand, 1984), and salinities that range from 12 in the upper portions of Great Bay and Little Egg Harbor, to 35 in lower estuarine stations that are not markedly seasonal (Able et al., 1992; Szedlmayer and Able, 1996). The annual input of freshwater into the drowned river estuary (Great Bay) and the barrier beach estuary (Little Egg Harbor) is low relative to the volume of the estuary (Chant et al., 2000; Durand, 1988). The primary source of ocean water moving into these estuaries is through Little Egg Inlet (4.6–8.8 m depth, salinity 28–35; Morse and Able, 1995). Little Egg Inlet also connects these estuaries to the adjacent inner continental shelf (3.0–16.5 m depth, in the vicinity of sand ridges, and 6.2–23.5 m depth, farther offshore; Morse and Able, 1995). The initial observations during 1992 evaluated settlement habitats by sampling planktonic (Tucker trawl) and recently settled (beam trawl) fishes to determine where initial use of benthic habitats (settlement) occurred (Able et al., unpubl. data). Based on this analysis, 9% of the fishes settled in the ocean, while 39% settled in the estuary, but a larger proportion (52%) settled in both habitats (Fig. 2). As part of the same sampling program, larger juveniles ( $>20$  mm) of a number of species were collected exclusively in estuarine habitats (50%), fewest in the ocean (19%) and a relatively large proportion (31%) in both habitats (Fig. 2).

In an independent analysis in the same area (Fig. 1), we compared juvenile fish use of estuarine and ocean beaches during 1998 and 1999 with seine collections (Fig. 3). Although there was some variation between years, the least frequently used juvenile habitat was the ocean (5% of species), the estuary was variable but intermediate (28–42%), and the largest proportion (52–67%) of species used both habitats in both years.

In a longer time series (1997–2002), the juvenile fishes using the same estuary and ocean habitats (Fig. 1), as sampled with an otter trawl, had a variable pattern

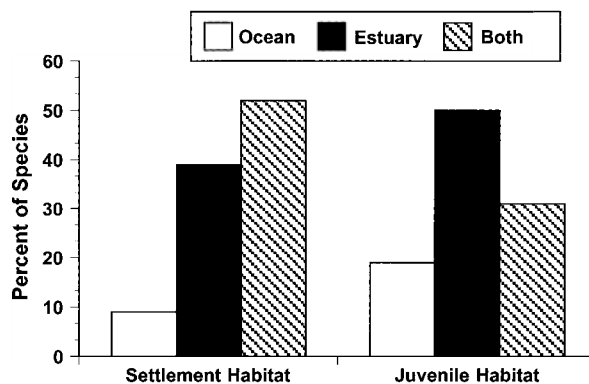


Fig. 2. Distribution of fish species using settlement and juvenile habitats across the estuary-ocean continuum based on 23 species that occurred in both ichthyoplankton (Tucker trawl) and benthic (beam trawl) sampling in 1992 (Able et al., unpublished. data). See Fig. 1 for sampling locations.

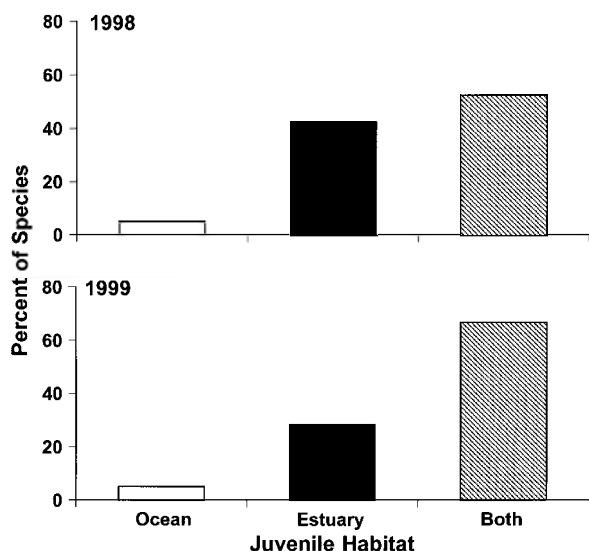


Fig. 3. Juvenile fish habitat use of ocean and estuarine beaches based on 39 (1998) and 40 (1999) species that occurred in seine samples in the vicinity of the Great Bay estuary in southern New Jersey (from Able et al., unpublished data). See Fig. 1 for sampling locations.

between years with the proportion of species exclusively using the ocean (30–54%) and the estuary (10–28%) ranging considerably, but in every year a large proportion of species (25–50%) were found in both habitats (Fig. 4). A more detailed analysis also suggests no obvious break between estuarine and ocean assemblages especially relative to the meso-polyhaline portions of the same estuary (Martino and Able, 2003). One might argue that a stronger salinity gradient at the estuary-ocean interface in this estuary might reveal a greater distinction in juvenile fish use between these habitats. On the other hand, the most obvious breaks in the fish assemblage occurred in the low salinity portion of the estuary (Martino and Able, 2003). The patterns observed for the entire assemblage are supported by focused autecological studies in the same area. Several species are known to use both estuaries and the coastal ocean as juvenile habitat including *Centropristis striata* (Able et al., 1995), *Prionotus evolans* and *P. carolinus* (McBride et al., 2002), *Pomatomus saltatrix* (Able et al., 2003), *Menticirrhus saxatilis* (Miller et al., 2002), *Gobiosoma ginsburgi* (Duval and Able, 1998), and *Syngnathus fuscus* (Lazzari and Able, 1990), while a smaller number of non-resident species appear to use the estuary exclusively as juvenile habitat including *Conger oceanicus* (Bell et al., 2003), *Paralichthys dentatus* (Able et al., 1990), and *Pseudopleuronectes americanus* (Curran and Able, 2002).

In summary, in this estuary-ocean comparison in southern New Jersey, a consistently large proportion of the fishes use both estuarine and ocean habitats as juveniles. Further, this seems to be the case for most of the dominant species in the Middle Atlantic Bight. In an

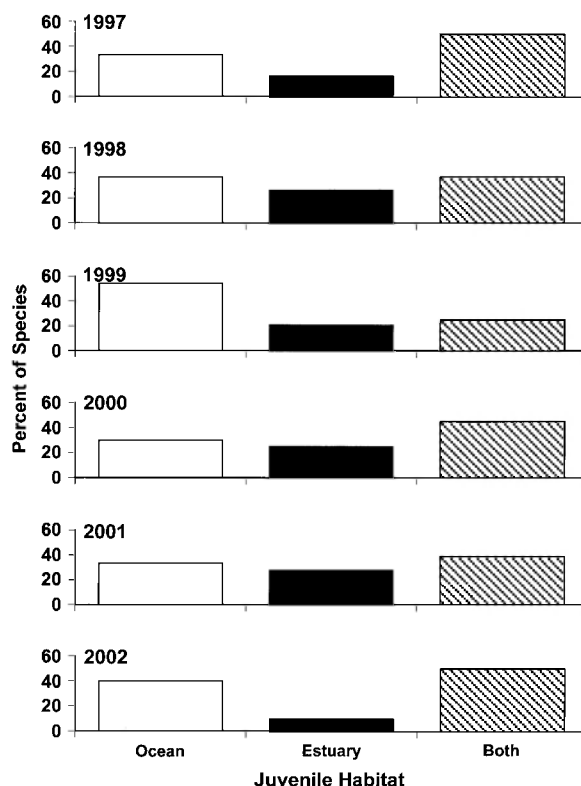


Fig. 4. Juvenile fish habitat use across the estuary-ocean continuum based on 18–24 species, depending on year, from otter trawl samples across a variety of habitats in the vicinity of Great Bay estuary in southern New Jersey during 1997–2002 (modified from Martino and Able, 2003 and unpublished data). See Fig. 1 for sampling locations.

earlier synthesis we attempted to categorize patterns of estuarine use for 70 of the dominant species (Able and Fahay, 1998). A reevaluation of these same species, based on the above sampling programs and the recent literature (some of it above), suggests that although there are a large number of estuarine obligate species, (45% e.g. cyprinodontids, fundulids), there are a similar number of species that use estuaries in a facultative manner (42.5%, e.g. those that use both the estuary and the ocean or estuarine use varies annually, geographically, etc.) (Fig. 5). Other species are insufficiently known to confidently characterize (12.5%) (Table 77.2 in Able and Fahay, 1998). Further, it is important to keep in mind that the patterns of habitat use are complex. As an example, we now know that the spring-spawned cohort of *Scophthalmus aquosus* use both the estuary and the inner continental shelf as juvenile habitat, but the fall-spawned cohort only uses the inner shelf (Neuman and Able, 2003). In yet another example of the difficulty of characterizing habitat use, it is clear that *Chaetodon ocellatus* settle, reside and grow in estuarine habitats in southern New Jersey, but these habitats are sinks because the young-of-the-year die when temperatures decline in the fall/winter, thus they contribute nothing to the adult population (McBride and Able, 1998).

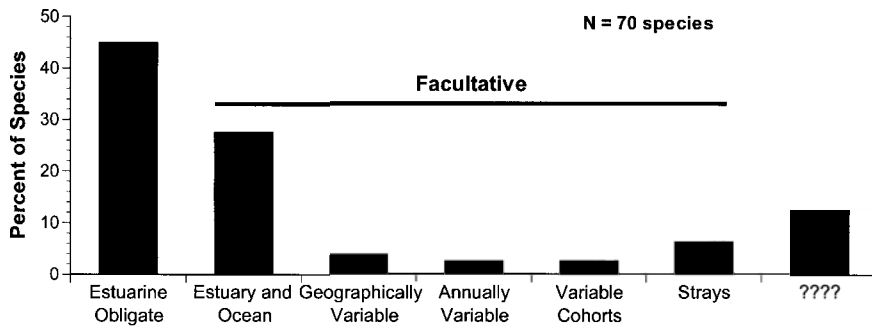


Fig. 5. Characterization of degree of estuarine dependence for representative Middle Atlantic Bight fishes based on data in Table 1.

### 6. Conclusions and future directions

Perhaps the simplest way to interpret “estuarine dependence” is to acknowledge that fish use of estuarine and oceanic habitats is a continuum (Fig. 6); some species have obligate life history stages (i.e. residents, diadromous) in the estuary, others are facultative users (estuarine opportunists) of the estuary, and still others are simply strays that occasionally find their way into an estuary. Most importantly, those fish which are facultative estuarine users may vary in their use on varying geographic, ontogenetic, annual and cohort-specific scales (Table 1).

This re-evaluation makes no pretense of reviewing all the literature that might bear on the question of estuarine dependence. Thus, further synthesis is necessary and should focus on the following concerns and questions. First, we need more information on patterns in different types of estuaries including hypersaline lagoons, permanent and intermittently open estuaries, and across a broad geographical range in order to

discern degree of estuarine dependency. Second, in each of these instances we need a better understanding of the functional significance of estuaries, and their habitats, relative to the ocean, e.g. across habitat landscapes. For example, just as “understanding the association between estuarine biota and habitat demands life history, physiological, and ecological knowledge of estuarine communities as they interact across the mosaic of estuarine landscapes” (Simenstad et al., 2000), this same approach is needed across the estuarine–ocean ecotone. Third, there is a need for more research of biotic factors (e.g. competition, predation, etc.) to enhance our understanding of estuarine dependence. Currently, this type of data is almost always lacking. Fourth, we need to determine how the degree of freshwater input into estuaries might influence available habitat and its distribution, especially with regard to the identification and importance of the offshore estuary but also relative to the use of the lower estuary by “ocean” species. One approach is to allow the differences in the fish fauna across the estuary-ocean ecotone to define the external

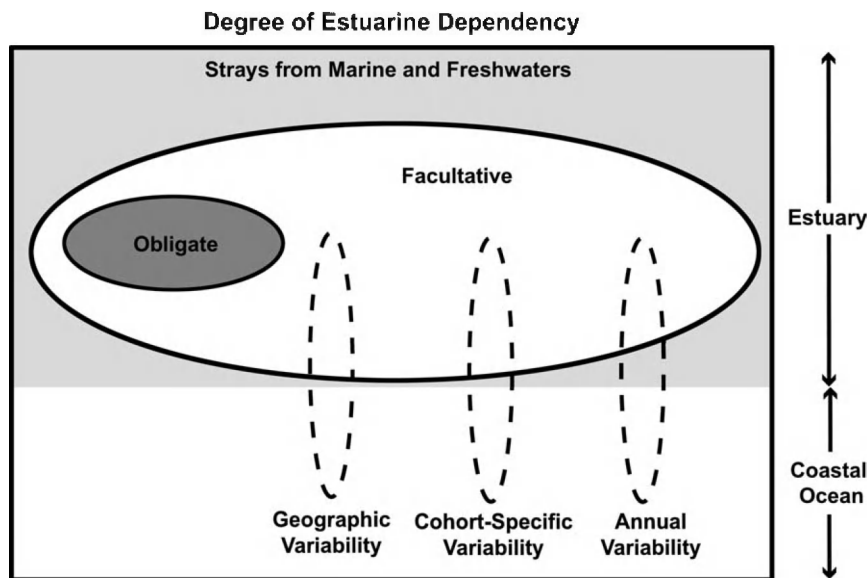


Fig. 6. Conceptual view of degree of estuarine dependency (obligate, facultative, strays) for fishes in the Middle Atlantic Bight. Among fishes that are facultative users of estuaries are those that vary geographically, annually or in a cohort-specific manner. See text for fuller explanation.

Table 1  
Degree of estuarine dependence for representative fishes in the Middle Atlantic Bight

Species	Degree of estuarine dependence				
	Obligate	Facultative			
		Estuary and ocean	Geographic variability	Annual variability	Cohort variability
<i>Mustelus canis</i>	X				
<i>Anguilla rostrata</i>	X				
<i>Conger oceanicus</i>	?				
<i>Alosa aestivalis</i>	X				
<i>Alosa mediocris</i>	X				
<i>Alosa pseudoharengus</i>	X				
<i>Alosa sapidissima</i>	X				
<i>Brevoortia tyrannus</i>	X				
<i>Clupea harengus</i>		?	?	?	
<i>Anchoa hepsetus</i>		X	?		
<i>Anchoa mitchilli</i>		X		?	
<i>Osmerus mordax</i>	X				
<i>Synodus foetens</i>					X
<i>Microgadus tomcod</i>	X				
<i>Pollachius virens</i>	?				
<i>Urophycis chuss</i>		X			
<i>Urophycis regia</i>		X		?	
<i>Urophycis tenuis</i>		X	?		
<i>Ophidion marginatum</i>		X			
<i>Opsanus tau</i>	X				
<i>Strongylura marina</i>	X				
<i>Cyprinodon variegatus</i>	X				
<i>Fundulus heteroclitus</i>	X				
<i>Fundulus luciae</i>	X				
<i>Fundulus majalis</i>	X				
<i>Lucania parva</i>	X				
<i>Gambusia holbrooki</i>	X				
<i>Membras martinica</i>		X	?		
<i>Menidia beryllina</i>	X				
<i>Menidia menidia</i>	X				
<i>Apeltes quadracus</i>	X				
<i>Gasterosteus aculeatus</i>	X				
<i>Hippocampus erectus</i>	X				
<i>Syngnathus fuscus</i>	X				
<i>Prionotus carolinus</i>		X			
<i>Prionotus evolans</i>		X			
<i>Myoxocephalus aeneus</i>		X	?		
<i>Morone americana</i>	X				
<i>Morone saxatilis</i>	X				
<i>Centropristis striata</i>		X			
<i>Pomatomus saltatrix</i>		X		X	
<i>Caranx hippos</i>		X			
<i>Lutjanus griseus</i>					X
<i>Stenotomus chrysops</i>		X	X		
<i>Bairdiella chrysoura</i>	X			X	
<i>Cynoscion regalis</i>		X			
<i>Leiostomus xanthurus</i>	X		?	X	
<i>Menticirrhus saxatilis</i>		X			
<i>Micropogonias undulatus</i>	X				
<i>Pogonias cromis</i>	X				
<i>Chaetodon ocellatus</i>					X
<i>Mugil cephalus</i>	X				
<i>Mugil curema</i>	X				
<i>Sphyrna borealis</i>	?				
<i>Tautoga onitis</i>	X				
<i>Tautoglabrus adspersus</i>		X			
<i>Pholis gunnellus</i>		?			
<i>Astroscopus guttatus</i>		?			
<i>Hypsoblennius hentz</i>	?				
<i>Ammodytes americanus</i>		X			



Table 1 (continued)

Species	Degree of estuarine dependence				
	Obligate	Facultative			
		Estuary and ocean	Geographic variability	Annual variability	Cohort variability
<i>Gobionellus boleosoma</i>					X
<i>Gobiosoma bosc</i>	X				
<i>Gobiosoma ginsburgi</i>		X			
<i>Peprilus triacanthus</i>		X	?		?
<i>Scophthalmus aquosus</i>		X	X		X
<i>Etropus microstomus</i>		X			
<i>Paralichthys dentatus</i>	X				
<i>Pseudopleuronectes americanus</i>	X		?		
<i>Trinectes maculatus</i>	X				
<i>Sphoeroides maculatus</i>		?			

Based on young-of-the-year habitat use as interpreted from Able and Fahay (1998) and unpublished data. ? indicates likely but not definitive degree of estuarine dependence. See text for further details.

boundary of the estuary much as has been done within estuaries (Bulger et al., 1993).

All of the above suggestions, and those of others (Haedrich, 1983; Weinstein, 1985; Able and Fahay, 1998) have to be viewed in the long term to understand the influence of episodic (storms, environmental perturbations, etc.) and long-term (climate, overfishing, habitat disturbance, etc.) events. Although attempts to address these questions were difficult in the past, development of in situ approaches such as coastal observatories (Glenn et al., 2000; Schofield et al., 2002), stationary (Gibson et al., 1998) and towed camera systems (Diaz et al., 2003), real-time tracking of fishes with active and passive arrays (O'Dor et al., 1998; Lembo et al., 2002; Grothues et al., submitted for publication), archival tags (Metcalf and Arnold, 1997; Kasai et al., 2000), and acoustic identification of spawning habitat (Luczkovich et al., 1999), now provide approaches that can significantly increase the likelihood of enhanced understanding of the connectivity between estuarine and ocean habitats that would have been inconceivable within recent history.

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