Visualisation of standardized life-history patterns

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Abstract

The life-history patterns of fish and invertebrate species are complex. But much of this complexity can be captured in simple diagrams of coastal transects, where juveniles usually occur in larger numbers in shallow waters, while adults generally inhabit deeper, offshore waters. Iconographic representations of generalized life-history patterns and depth profiles, with specific key life-history parameters can capture much of these standardized patterns, including spawning areas, nursery/juvenile distributions, adult distributions and spawning migrations. Several examples presented here from a wide range of habitats and ecosystems (temperate and tropical waters, demersal, deep water, pelagic and coral reefs), including an example of different stocks of the same species, illustrate some general patterns with regard to water depth and distance from shore. The present approach should be viewed as a first step towards obtaining standardized patterns about key life-history parameters, and will hopefully lead to incorporation into management of life-history interconnectivity between different fishery sectors or gears. This may contribute to sustainable, ecosystem-based approaches to management by informing policy options when faced with decisions to rationalize overcapitalized fisheries.

Keywords coastal transects, depth distribution, fish ecology, life-history patterns, temperate, tropical, visualization

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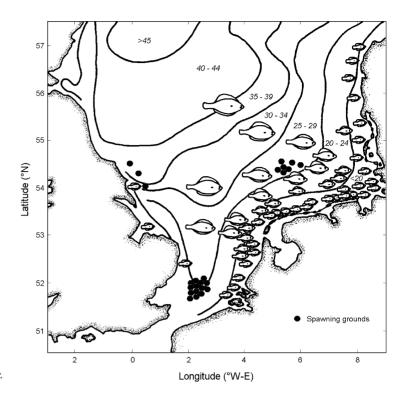


Figure 1 Schematic representation (geographical map view) of the distribution of plaice (*Pleuronectes platessa*) in the North Sea (modified after Garstang 1909). Mean sizes (cm TL) are given for each depth isobar.

Introduction

Life-history patterns of marine resources are generally viewed as multidimensional in scale, with complex interactions between components defined by ecology, oceanography, time and geography. Often this complexity has made it difficult to assimilate potential effects of extractions on a species and the industry it supports. This may be either owing to the perception of multidimensional complexity being thought intractable, or because of an oversight of basic patterns.

Here, we argue that this multidimensional complexity can be reduced to a simpler, generalized twodimensional life-history pattern, while still capturing the essential information. Both Charles Darwin and Alexander von Humboldt used the method of reduced dimensionality to focus their readers attention to the key issues while capturing most of the significant information concerning the topic at hand. For example, after reviewing much literature, Darwin concluded that "latitude is a more important element than longitude" for explaining the distribution of organisms (Barrett *et al.* 1987). This concept has recently been revisited in a latitudinal analysis of population dynamics and ecology of flatfishes (Pauly 1994). It was Humboldt, however, who in his classic

Voyage aux régions équinoxiales du Nouveau Continent first used a transect technique to visualize the advantage of reduced dimensionality in explaining observed patterns in distribution (Gayet, pp. 2284-2287 in Tort 1996). Here, we present an approach to standardize life-history patterns, using reduced dimensionality, that will permit discovery of concepts and generalities that might otherwise be lost in the clutter of overparameterization and specific details. Similarly, standardization to discover ecological patterns and propensities from a multitude of data and detailed patterns have been used by R. Myers in his meta-analysis approach of recruitment rates (e.g. Myers et al. 1999), by Cury and Roy (1989) for relationships between environmental parameters (especially wind strength) and pelagic fish recruitment success, and by Pauly (1998) for general patterns of growth in fishes. In fisheries science, a classic example of data suitable for reduced dimensionality was presented by Garstang (1909) for the North Sea plaice (Pleuronectes platessa, Pleuronectidae, Fig. 1). Heincke (1913) re-expressed this as a 'law' wherein size increases with distance from shore (and depth), while numbers decline.

The life-history characteristics of many species and stocks show generalized two-dimensional patterns, involving water depth and distance from shore. In an analysis of broad-scale patterns of biomass in the

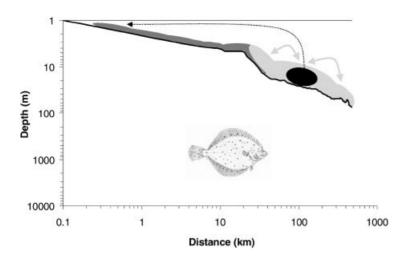


Figure 2 Generalized life-history pattern by depth zone for North Sea plaice (*Pleuronectes platessa*). Black contour line represents a typical depth transect from approximately 53° N, 8° E to 56° N, 3° E. Dark grey represents juvenile distribution, light grey represents adult range and black indicates spawning strata.

North Atlantic, depth and distance from coast (while correlated) were shown to be independent enough to require inclusion of both parameters in a Generalized Linear Model (V. Christensen, personal communication). FAO (1972) used the depth and distance from coast approach for many species in their Atlas of the Living Resources of the Seas, and Pauly (1982) indicated such a pattern for the fishes of a tropical bay. It is recognized that, for many applications, an inshore/ offshore axis may better convey information on general structure and processes than an alongshore axis or general geographical map view (Pauly and Lightfoot 1992). A good example of this is demonstrated by comparison of Garstang's map-view of plaice size distribution in the North Sea (Fig. 1) with our representation of the same information for the same species and area using a standardized two-dimensional graph of water depth vs. distance from shore (Figs 2 and 3). Such a transect approach permits the use of icons to represent key processes or patterns, as well as standardization of axis (e.g. log scale), which enables most species or stocks to be directly compared across extensive depth and distance scales. Obviously, in certain circumstances, and especially for regional stock assessment purposes, map based spatial knowledge that is more location-specific is required. However, our aim here is to demonstrate a standardized approach to illustrate that patterns that are perceived to be complex or different between species or stocks if looked at individually and in close-up focus, are in essence often very similar with regards to certain key parameters. It is thus a question of finding what might be called 'axes of functionality' that explain the general properties and patterns that are shared between species.

For our coastal transects we used species and stockspecific data summarized from standard literature searches, as well as species-specific searches of FishBase (Froese and Pauly 2000). For brevity, only broad summaries of this information are included here. The depth transects were obtained from ground-truthed

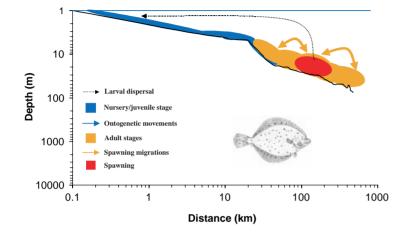
Figure 3 Generalized life-history pattern by depth zone for North Sea plaice (*Pleuronectes platessa*). Black contour line represents typical depth transect from approximately 53° N, 8° E to 56° N, 3° E. Colour and symbol codes are shown in the key.

Figure 4 Generalized life-history pattern by depth zone for Norwegian spring spawning herring (*Clupea harengus*) prior to the stock collapse in the late 1960s early 1970s, and the currently re-established pattern. Black contour line represents typical depth transect from approximately 63° N, 8° E to 67° N, 11° W. Colour and symbol codes as per Fig. 3.

Figure 5 Generalized life-history pattern by depth zone for Barents Sea and Norwegian coastal cod stocks (*Gadus morhua*). Black contour line represents typical depth transect from approximately 68° N, 13° E to 76° N, 18° E. Note transect is running in a NNE direction and not at right angle to Norwegian coastline. Colour and symbol codes as per Fig. 3.

Figure 6 Generalized life-history pattern by depth zone for Gulf of Maine and Georges Bank cod stocks (*Gadus morhua*). Black contour line represents typical depth transect from approximately 42° N, 70° W to 40° N, 65° W. Colour and symbol codes as per Fig. 3.

Figure 3



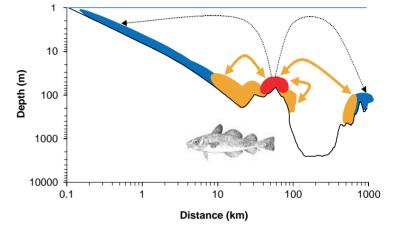
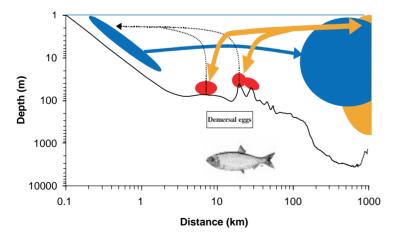
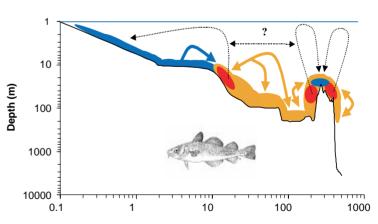


Figure 5





Distance (km)

Figure 6

depth data (standardized to Mean Sea Level; P. Sloss, NOAA-NGDC, personal communication) with a twonautical mile resolution based on satellite sources ('Global Relief' NOAA-NGDC, MGG Division, Boulder, Colorado, USA). The depth contour data were used in the Surfer geo-statistical program to calculate depth contours between locations relating to the general geographical area being considered (R. Watson, Fisheries Centre, University of British Columbia, Vancouver, personal communication). Thus, individual bottom contour transects are representative depth contour transects derived from the stock-specific geographical area. Graphs are standardized to logscales to permit most species and stocks to be directly comparable across extensive depth (1-10000 m) and distance scales (0.1-1000 km), while simultaneously permitting shallow water, near-shore areas to be represented where applicable. The orientation of the inshore/offshore axis relative to the coastline is clearly a fractal problem of spatial scale of coastline (e.g. Jiang and Plotnick 1998). Given the large spatial scale covered by our transects (up to 1000 km offshore), the orientation of transects were typically at right angles to the average regional coastline, as indicated by large-scale GIS maps (Surfer geo-statistical program), unless otherwise indicated.

It might be questioned why we chose iconographic visualization as a vehicle to present these patterns and the message associated with them. A clear advantage of standardized, two-dimensional graphs over map-view is that they permit standardized comparison between different examples at one glance (Pauly and Lightfoot 1992). Moreover, Tufte (1983) suggested that: "... of all methods for analysing and communicating information, well-designed data graphics are usually the simplest and at the time the most powerful. Excellence in statistical graphics consists of complex ideas communicated with clarity, precision, and efficiency." While these graphs can also be presented in shades of grey (Fig. 2), we adhered to Tufte's theory of information presentation, designing the graphs to be easy to decode by the viewer (incorporating hues chosen to permit easy decoding by colour-deficient viewers, Tufte 1983, p. 183), contain key information (four major life-history stages) and are standardized in scale, to permit direct comparison between species and areas.

Four key life-history stages are presented in the colour graphs: larval dispersal indicated by black dotted arrows (from hatching or larval extrusion to settlement or early juvenile stage); juvenile stages in blue (from postlarval to prefishery-recruitment stages); adult stage in brown (recruited to fishery); and spawning depth strata in red (representing depth zones used preferentially for spawning). Additional arrows may indicate ontogenetic movements (blue), regular spawning migrations (brown), or major water currents of ontogenetic significance (grey). The larval stage is being represented as a flow arrow only, to illustrate the link, via larval stage, between spawning areas and juvenile nursery habitats.

Below, we present several examples from temperate and tropical waters to illustrate the universal applicability of this standardized approach. We also indicate (with one example) the suitability of this approach to compare stocks of the same species from different geographical regions.

Case studies

The species illustrated here represent an arbitrary choice of very important fisheries species. They were selected to cover a wide range of marine ecosystems (temperate as well as tropical waters) and habitats (demersal, pelagic, deep waters, coral reefs), and include fishes as well as an invertebrate example. The species covered are: North Sea plaice (*Pleuronectes platessa*, Pleuronectidae); Atlantic herring (*Clupea harengus*, Clupeidae); Atlantic cod (*Gadus morhua*, Gadidae); Deepwater redfish (*Sebastes mentella*, Sebastidae); West Australian rock lobster (*Panulirus cygnus*, Palinuridae); Coral trout (*Plectropomus leopardus*, Serranidae); and the Splendid ponyfish (*Leiognathus splendens*, Leiognathidae).

Temperate waters

North Sea plaice

The Plaice (*Pleuronectes platessa*) is a right-eyed flatfish occurring commonly in the North-east Atlantic (Garstang 1909; McKeown 1984; Froese and Pauly 2000). In the North Sea, four major spawning subgroups are recognized: Scottish east coast, Flamborough, Southern Bight and German Bight spawning groups (McKeown 1984 and references therein). Plaice spawn in 25–75 m depth, eggs and larvae are pelagic for approximately 3–8 weeks, and metamorphose to juveniles which settle in nursery areas in shallow, coastal waters (Muus and Dahlstrøm 1977; McKeown 1984, Figs 2 and 3). Juveniles remain in shallow waters (< 20 m) for the first few years, then start moving into deeper waters. Plaice reach sexual maturity at 3–4 years, then undertake their first migration to spawning areas. Thereafter they disperse over a larger area, mainly in deeper waters, with overlap with other plaice stocks (McKeown 1984).

Atlantic herring

Herring populations (Clupea harengus) often display complex feeding and spawning migrations (Iles 1971). They are separated into numerous local 'races', often identified by spawning locations and spawning periods (e.g. North Sea spring spawning herring; Muus and Dahlstrøm 1977; McKeown 1984; Blaxter 1985). Areas suitable for spawning by herring are banks and coastal areas with stony and rocky bottom and depths less than 250 m (Slotte and Fiksen 2000). Herring eggs are demersal (Blaxter 1985) and larval duration range from 2 to 6 months depending on stock (Houde and Zastrow 1993; Froese and Pauly 2000). Research on herring life history indicates that in many cases there is considerable mixing, both in the nursery areas and feeding grounds of different populations, while segregation occurs during spawning and early larval stages (Iles 1971; Iles and Sinclair 1982; Sinclair and Iles 1985; Sinclair et al. 1985).

The Arcto-Scandian herring stock (now called Norwegian Spring Spawning herring) displays extensive seasonal and ontogentic migrations, and may serve as a pelagic example (Fig. 4). Spawning areas are along the south-western and western Norwegian coast. Herring larvae drift to a variety of nursery grounds in coastal fjords and the Barents Sea. Adult feeding and over-wintering areas are offshore as far as Faroe Islands, Jan Mayen Island and Iceland (FAO 1972 maps 2.2 and B.2, Muus and Dahlstrøm 1977; Slotte and Fiksen 2000). In the 1990s the Norwegian Spring Spawning herring stock has recovered from near extinction in the late 1960s, and appears to have re-established most of its previous patterns. However, for nearly 25 years after the collapse, the oceanic nursery, feeding and wintering areas (Barents Sea, Iceland and Norwegian Sea) were abandoned, and the entire life cycle was spent in Norwegian coastal waters and fjords (Dragesund et al. 1980; Rottingen 1990; Holst et al. 1998; Slotte and Fiksen 2000).

Atlantic cod

The Atlantic cod (*Gadus morhua*) is a diurnally schooling, demersal or benthopelagic species, occurring from shoreline to 500–600 m depth (FAO 1972, map B.1; Muus and Dahlstrøm 1977; Cohen *et al.*

1990; Froese and Pauly 2000). It can undertake long-distance migrations (FAO 1972, map 2.1; Cohen et al. 1990). Here we present examples of two stocks of Atlantic cod to illustrate the suitability of the standardized approach for intraspecies comparisons. One of the examples is from the north-east Atlantic (Barents Sea stock) and the other is from the west Atlantic (Gulf of Maine/Georges Bank). Spawning takes place in 50-150 m depth for Barents Sea stock (Fig. 5), as well as for Gulf of Maine/Georges Bank stocks (Serchuk et al. 1994; Fig. 6). During the spawning season adults are highly aggregated and closely associated with banks or shelf-edge features (spawning areas), whereas during the nonspawning season distribution is more widely dispersed (Frank et al. 1994). Cod eggs are pelagic and concentrate in the 0-10 m depth strata, larvae hatch within 2-4 weeks of spawning, and settlement occurs after 3-5 months at 3-6 cm in size (Muus and Dahlstrøm 1977). Historically, sexual maturity was reached at between 4 and 15 years, however, currently this is reduced to 1-7 years owing to overfishing (Serchuk et al. 1994; Longhurst 1998). Historic longevity was approximately 25 years, maximum size c. 200 cm (Muus and Dahlstrøm 1977). Cod in northern Norway (Fig. 5) are considered as two entities, although managed as a single stock: Norwegian Coastal cod and Barents Sea stock (Fyhn et al. 1994; Loken et al. 1994). Loken et al. (1994) compared Barents Sea cod with Coastal cod stocks in Norway, and found different early life histories, but no conclusive indication of different stock structure. Barents Sea cod juveniles remain planktonic for longer and settle far to the north and east in the Barents Sea (McKeown 1984; Helle 1994; Loken et al. 1994), while coastal cod juveniles settle earlier in very shallow coastal waters where the macroalgal belt might provide protection from predation (Loken et al. 1994). Similar shallow water settlement is also observed in North Sea cod (Riley and Parnell 1984 in Loken et al. 1994). Juvenile cod (1-year-old) have been reported to inhabit the shore slope of fjords between 10 and 30 m depth (Svendsen 1995). In the western Atlantic (e.g. Georges Bank), as well as on other shelf areas, most cod larvae appear to be retained on the banks used as spawning areas owing to hydrodynamic patterns (Anderson et al. 1995; Fig. 6) and the early stage of larval activity assists movements shoalwards (Serchuk et al. 1994). Juvenile cod (1-year-old) have been reported to inhabit the shore slopes of Norwegian fjords between 10 and 30 m depth (Svendsen 1995). Coastal cod within the Gulf of Maine (Fig. 6) appear to maintain their own spawning grounds (e.g. Sheepscot Bay), and show an affinity to shallower (< 100 m) coastal areas (Perkins *et al.* 1997).

Deepwater redfish

In the North Atlantic, there are two main species of redfish, Sebastes mentella (deepwater redfish, ocean perch) and S. marinus (golden redfish), which overlap in occurrence (FAO 1972, map A.1; Christensen and Pedersen 1989). A third species (S. viviparus) is generally found in shallower waters, and is the most common redfish in the North Sea and the Skagerrak (Anonymous 1998). Similarly, a third species (S. fasciatus, Ascadian redfish) occurs in the western Atlantic, also primarily in shallow waters in inshore areas (mainly 10-30 m depth, Kelly and Barker 1961 in Kenchington 1991), and is very common in the Gulf of Maine (Scott and Scott 1988). Here we concentrate on the first species, the deepwater redfish S. mentella (Fig. 7). As its common name suggests, S. mentella is a deepwater, predominantly benthic species that rises off the bottom during the night (Scott and Scott 1988). However, mesopelagic aggregations have been documented in the Irminger Sea (Fig. 7), and might represent separate stocks (Bel'skiy et al. 1987; Christensen and Pedersen 1989).

Depth range of occurrence for *S. mentella* is 130– 900 m (Froese and Pauly 2000), and stocks often show stratification by depth, with smaller individuals generally more shallow (Christensen and Pedersen 1989). Immature individuals have been recorded widely distributed down to 500 m (Drevetnyak 1993). However, no change in average length with depth was recorded for depths between 150 and 200 m, but average size did increase with depths of > 200 m

(Magnusson et al. 1990). Redfish are ovoviviparous and larvae are born (extruded) at approximately 7 mm size after absorbing the yolk-sac. During the larval extrusion period adults were found at 250-700 m depth (Drevetnyak 1993), with the majority of extrusions occurring at 250-400 m depth (Magnusson et al. 1990; Mukhina et al. 1992, 1995). The larval stage is pelagic in surface waters in 0-50 m depth (Christensen and Pedersen 1989; Herra 1989; Mukhina et al. 1992). Nursery areas are found mostly at depths between 50 and 350 m (Anonymous 1998). At approximately 25 mm in size they start moving into deeper waters (Christensen and Pedersen 1989). Redfish grow to 7-8 cm during their first year, thereafter approximately 2.5 cm per year until about 10 years of age, after which growth slows down (Scott and Scott 1988). Sexual maturity is thought to be reached at 8-10 + years of age, with a longevity of 40 + years (Christensen and Pedersen 1989).

Subtropical and tropical waters

West Australian rock lobster

The western rock lobster (*Panulirus cygnus*) occurs off the western Australian coast, where they inhabit (postlarval to adult) the continental shelf from 1 to 200 m depth, with highest densities in waters less than 60 m (Kailola *et al.* 1993; Fig. 8). They support one of the worlds largest lobster fishery, averaging over 10 000 t per year, which is the most lucrative single-species fisheries in Australia (Phillips *et al.* 1994).

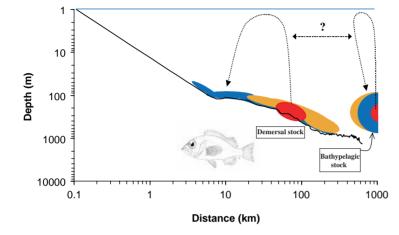
Larval stages are dispersed up to 1500 km offshore and spend almost a full year in the south-eastern Indian Ocean. Thereafter, the late larval stages return to the continental shelf, where they metamorphose to the puerulus stage which crosses the shelf

Figure 7 Generalized life-history pattern by depth zone for Irminger Sea deepwater redfish stocks (benthic and mesopelagic *Sebastes mentella*). Black contour line represents typical depth transect from approximately 63° N, 22° W to 59° N, 30° W. Colour and symbol codes as per Fig. 3.

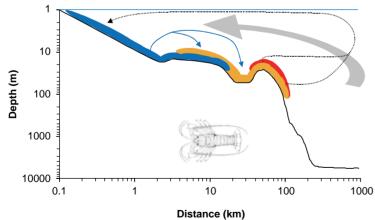
Figure 8 Generalized life-history pattern by depth zone for the West Australian rock lobster stock (*Panulirus cygnus*). Black contour line represents typical depth transect from approximately 27° S, 114° E to 29° S, 110° E. Colour and symbol codes as per Figure 3. The large grey arrow indicates the effect of the Leeuwin current on larval dispersal.

Figure 9 Generalized life-history pattern by depth zone for coral trout, also called coral grouper (*Plectropomus leopardus*). Black contour line represents typical depth transect from approximately 20° S, 148° E to 17° S, 158° E. Colour and symbol codes as per Fig. 3.

Figure 10 Generalized life-history pattern by depth zone for the splendid ponyfish (*Leiognathus splendens*). Black contour line represents typical depth transect from approximately 13° N, 123° E to 19° N, 123° E. Colour and symbol codes as per Fig. 3.









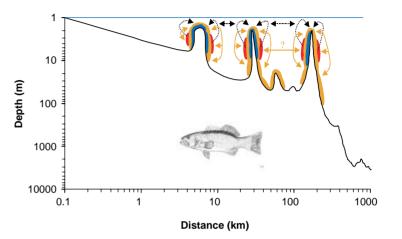


Figure 9

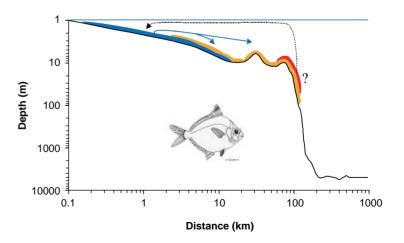




Figure 10

and settles on shallow coastal reefs, in waters less than 30 m (Kailola et al. 1993; Phillips and Pearce 1997). The annual level of settlement is related to the strength of the local Leeuwin current, by increasing transport to the coast (Fig. 8). Juveniles remain on shallow coastal reefs for 3-6 years before recruiting to the fishery in the deeper, adult habitats (Phillips et al. 1991; Kailola et al. 1993). The maximum distance recorded during juvenile-adult migration was approximately 170 nm (Kailola et al. 1993). Rock lobster are nocturnal, omnivorous foragers, and tagging studies of preadult stages indicated a wide range of movements, with 67% of lobsters traveling almost directly offshore (Phillips 1983; Anonymous 1984). Adults mate between July and December, and females carry the spermatophores until eggs are spawned between August and January in the deeper parts of the adult range (Kailola et al. 1993).

Coral trout

The common coral trout [Plectropomus leopardus (Serranidae)] is one of seven species of Plectropomus (also called coral groupers) occurring in the Indo-Pacific. Plectropomus leopardus inhabits tropical western Pacific waters from southern Japan to Australia, west to Indonesia and east to Fiji (Randall and Hoese 1986). On the Australian Great Barrier Reef (GBR) they inhabit waters from 1 to 100 m depth, from inshore reef areas to steep outer reef margins (Kailola et al. 1993; Fig. 9). Adult P. leopardus occupy home ranges that are on average $10500-18800 \text{ m}^2$ in size, depending on reef habitat (Zeller 1997). Plectropomus are protogynous hermaphrodites, and spawning occurs in spring-summer at multiple spawning aggregations per reef at depths of 6 m to at least 25 m (Samoilys and Squire 1994; Samoilys 1997; Zeller 1998). Common coral trout undertake regular migrations to their respective aggregation sites, and display site fidelity (Zeller 1998). The planktonic larval stage takes 3–4 weeks in GBR waters (Doherty et al. 1994), and larvae are also found over habitats similar to adult coral trout. Common size at settlement is c. 16-17 mm (SL), with 2-month-old juveniles reported as 45-85 mm (SL) (Brown et al. 1991). Demersal juveniles inhabit shallow reef waters in and around reef areas, primarily in coral rubble areas $> 5 \text{ m}^2$ (Brown *et al.* 1991; Light and Jones 1997), and have been observed at the base of emergent reef structures at depths of 10-15 m (D. Zeller personal observation). Large adult coral trout are reported to inhabit deeper waters (> 20 m) outside of spawning periods, but move into shallower water to feed (McPherson *et al.* 1988).

Splendid ponyfish

The splendid ponyfish (Leiognathus splendens), a small schooling species, is widely distributed throughout the coastal waters of the tropical and subtropical Indo-Pacific (Jones 1985). It has a strong preference for turbid inshore areas (Fig. 10), and forms an important component of the demersal fish assemblages in the tropical Indo-Pacific region (Jones 1985). It has been recorded at depths of 5-100 m (Pauly 1977; Froese and Pauly 2000). Leiognathids often numerically dominate demersal trawl catches in waters less than 30 m (McManus 1986) and often form relatively important fisheries, particularly in developing countries (Pauly 1977). In South-east Asian waters the commercially most important concentrations occur in 20-40 m, with isolated schools between 40 and 60 m (Pauly 1977). Juveniles have been reported from estuaries, whereas adults are found predominantly outside estuaries in coastal waters (Pauly 1982).

Discussion

The purpose of the generalized life-history transect approach presented here is not to document a detailed, quantitative depth distribution analysis. Rather, it is meant to focus attention on the broad, underlying patterns of generalized life histories of marine resources, and to illustrate the interconnectivity, through life-history stages, of coastal and offshore marine environments over large distances. However, the present graphical format lends itself to inclusion of additional quantitative data in the form of vertical and horizontal data graphics that can be incorporated into the existing transects. Such quantitative information can be obtained from various sources, such as depth-stratified survey data (e.g. Mahon and Sandeman 1985; Mahon et al. 1998). Additional information, such as seasonal variation in distribution or temperature iso-lines can also be accommodated, for example through multipanel graphics. Of particular importance for the practical application of the present approach might be the incorporation, in the form of additional horizontal data graphics, of relative fishing effort intensity by various gear types (based on fishing ground information and gear-specific fishing depths) or fisheries sectors (small-scale coastal, large-scale offshore). Thus, the standardized approach presented here might become useful to illustrate the interaction and competition between fisheries sectors or gears in a visually clear and standardized manner. Such clear and distinct visualizations might assist management in the formulation of more informed policy options for ecosystem-based management of fisheries.

There are numerous additional purposes for which the present visualization of two-dimensional life-history patterns may be used. For example, we currently utilize this approach as a component of the assessment of ecosystem effects of fishing undertaken by the Sea Around Us Project at the University of British Columbia Fisheries Centre (www.fisheries.ubc.ca). Within the framework of this project, such coastal transect distributions and depth information help in assigning fisheries catches to areas such as those described in the classification systems of Large Marine Ecosystems (Sherman and Duda 1999) and 'biogeochemical provinces' (Longhurst 1995), utilizing the known and preferred depth distribution for each species. A consensus synthesis approach to these classification systems is being used by the Sea Around Us Project (see Pauly et al. 2000). The catch data spatial allocation algorithm also uses augmentative data on geographical distribution and quantitative depth information where available (e.g. cumulative distribution frequency curves in Perry and Smith 1994). Application of the approach presented here in the context of this project involves the use of such standardized life-history patterns in large scale database analyses to spatially refine official FAO catch statistics (Watson et al. in press).

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