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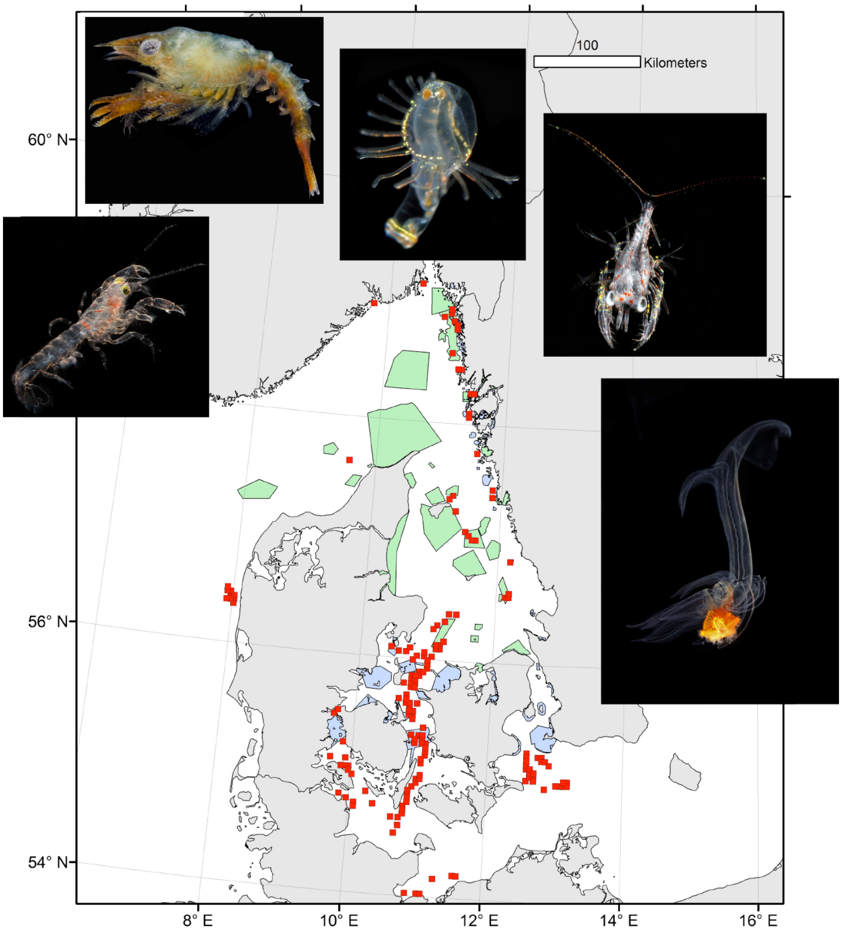

LARVAL CONNECTIVITY AND ECOLOGICAL COHERENCE OF MARINE PROTECTED AREAS (MPAs) IN THE KATTEGAT-SKAGERRAK REGION

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Larval connectivity and ecological coherence of marine protected areas (MPAs) in the Kattegat-Skagerrak region

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PREFACE

Marine protected areas (MPAs) are considered effective instrument to mitigate the loss of biodiversity in the sea. However, the management of MPA-networks is challenged by a lack of information of habitat distribution, and of how populations are connected between habitats and MPAs through dispersal of pelagic larval stages.

In this study, the effect of larval connectivity on the ecological coherence of the MPA-networks in the Kattegat-Skagerrak area of the North Sea is investigated with special focus on the OSPAR-MPAs. By using biophysical models, the larval dispersal and connectivity of benthic organisms in the Kattegat-Skagerrak area is assessed. The report also aims to assess if a series of new model tools can be applied to identify optimal MPA-networks for benthic communities, and evaluate the existing MPA-networks with regards to larval connectivity.

This report was prepared on request by the Swedish Agency for Water and Marine Management.

Per-Olav Moksnes, Per Jonsson, Martin Nilsson Jacobi, Kevin Vikström
Göteborg, 4 April 2014

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EXECUTIVE SUMMARY

Background

Marine protected areas (MPAs) are considered effective instruments to mitigate the loss of biodiversity and to restore overexploited stocks. The OSPAR Commission and the Helsinki Commission (HELCOM) aim to establish a network of well-managed and ecologically coherent MPAs to preserve biodiversity in the Northeast Atlantic and the Baltic Sea, respectively. However, the management of MPA-networks is challenged by a lack of information of habitat distribution, and of how populations are connected between habitats and MPAs through dispersal.

Most marine organisms have pelagic larvae or spores that spend weeks or months drifting in the water column, potentially dispersing large distances (10s to 100s of km). The transport of larvae among populations is a complex function of ocean circulation, duration of the pelagic stage and the drift depth of the larvae, which could result in large differences in dispersal between species and areas. However, our understanding of larval dispersal and connectivity among local marine populations is extremely poor. It is therefore unclear whether a single MPA is large enough to allow settlement and recruitment within the MPA, or whether the distances between MPAs in a network are short enough to connect populations of targeted organisms. This lack of understanding creates serious problems both for the design and evaluation of functional MPA-networks.

This study has been prepared on request of the Swedish Agency for Water and Marine Management, SwAM to inform the analysis of ecological coherence of MPAs in the Kattegat-Skagerrak area with more detailed scientific information. The overall aim of the study is to use empirical data on larval traits and model tools to describe the larval dispersal and connectivity of benthic organisms in the Kattegat-Skagerrak area of the North Sea to evaluate the effect of larval connectivity on benthic communities within the MPA-networks in the area, with special focus on the OSPAR-MPAs.

Methods

The study was carried out in 4 steps. First, a unique library of larval traits of species found in the Kattegat-Skagerrak area was created by compiling a large empirical dataset consisting of over 300 depth-specific plankton samples from the study area. A total of 45 and 80 larval taxa and stages of fish and invertebrates, respectively, were collected and identified. The result showed that most taxa were concentrated in the water column at species-specific depths, and with a distinct seasonality in larval abundance. These results, together with a review of the literature were used to create realistic larval-types for the model study that would represent selected species groups of the targeted benthic communities.

In the next step, the dispersal of the selected larval-types was simulated using a 3-D ocean circulation model of the study area, coupled with a particle-tracking model. Based on empirical data on larval traits, we assessed the dispersal and connectivity of 14 different virtual larval types representing the selected groups of benthic organisms. Model trajectories of each larval type were released from all areas of the model domain between 1–100 m depth (in total ca. 9000 sites) twice per month for a total of 8 years. In total 335 million trajectories were modeled in the study. The connectivity of larval trajectories was assessed in three separate habitat scenarios: (1) between all areas of the model domain (1–100 m depth), (2) between only shallow (1–20 m) hard bottom habitats, and (3) between only deep (21–100 m) hard bottom habitats in the study area. The results were used to generate detailed connectivity matrices for both individual larval types and communities between different habitats and between MPAs.

In the third step, we used the connectivity matrices and a new method using eigenvalue perturbation theory (EPT) to identify the optimum network of MPAs with respect to the larval connectivity for all different larval types and habitat-combinations. In addition, we applied a novel EPT-method to identify the optimum network for 4 different communities of species with different dispersal strategies and connectivities.

In a last step, we evaluated the EPT-generated networks by comparing them with the present real-world MPA networks using a simple metapopulation model based on the connectivity matrices. In the model we simulated the effect of MPA-protection by giving populations within MPAs 20 % higher reproduction than populations outside the protected areas. The total size of the metapopulations in the study area was then compared between the different networks during periods of low abundance over a 100-year simulation.

Results and discussion

The model results demonstrated that larval dispersal distances were strongly affected by the drift depth and the pelagic larval period, as well as by the area from where they had been released in the model. Trajectories drifting at the surface were transported 2–10 times further (80–140 km in most areas after 30 d) and often in a different direction compared to trajectories drifting below the pycnocline at 24–26 m depth. However, for the same larval type, the average dispersal distance varied >100x between different areas of the Kattegat and Skagerrak. These strong regional differences, and large effects of larval traits on larval dispersal distances suggest that the potential for self-recruitment within MPAs will be strongly dependent on the local oceanographic conditions and the larval traits of the targeted species. It therefore not very useful to assess connectivity between MPAs with a fixed distance, as has been the praxis so far in evaluations of ecological coherence of MPA-networks.

The results also revealed an estuarine circulation in the study area where surface water was transported mainly northward in Kattegat and along the coast of Sweden, and west out of the model domain along the south coast of Norway, whereas deep water below the pycnocline was transported southward along the west coast of Sweden. This circulation had important consequences for the connectivity of populations with different larval traits in different regions. For example, the model results suggest that organisms living on shallow hard bottom habitats along the NW of Sweden with larvae drifting in surface water will receive larvae and new recruits mainly from western Kattegat, whereas the larvae released by the organisms are mainly transported to southern Norway and out of the study area. In contrast, organisms living on deep hard bottom habitats along the NW of Sweden with larvae drifting below the pycnocline will mainly receive larvae from populations within the region and from western Skagerrak area, whereas the larvae released to a large extent are transported southward to hard bottom habitats in northern Kattegat.

This asymmetric connectivity had large effects on the optimal MPA-network in the study area. Because many virtual larvae along the Swedish NW coast and Norwegian south coast were transported out of the Kattegat-Skagerrak area, few sites were selected from these areas in the optimal MPA-network based on larval connectivity. For most larval types, the EPT-model instead suggested a network with a majority of MPA-areas placed in western Kattegat, the Danish straits, and (when hard bottom habitats were not a requirement) the North Sea area along the west coast of Jutland. The optimal networks showed large differences between different larval types and habitats. For example, networks for shallow hard bottom organisms with MPAs placed in Skagerrak was only found for larval types with short PLD. In general, modeled larvae with large dispersal distance (surface drifter with long PLD) had a fewer number of selected sites within the Kattegat-Skagerrak area than larvae with short dispersal distances (deep drifters with short PLD), particularly for deep habitats (21–100 m).

Comparing the optimum networks of MPAs for communities of shallow and deep water organisms selected with the EPT-method with present real-world MPA networks showed large differences in distribution and the protective effects of the MPAs on the metapopulations in the study area. According to the results from the metapopulations models, the EPT-selected MPA-networks provided approximately 300–600 % better protection than the OSPAR-networks of the same size for shallow and deep hard bottom organisms. The OSPAR MPA-network perform similar to a randomly chosen MPA-network for shallow hard bottom organisms, but approximately 70 % better than a random network for deep hard bottom organisms, in particular in the NW coast of Sweden (300 % better). Including also non-OSPAR MPAs in the network improved the protection slightly compared to a random network of a similar size, but the EPT-networks were still approximately 200–500 % better. Surprisingly, the EPT-networks with MPAs mainly in SW Kattegat and the

Danish straits, and very few in the Skagerrak area still provided better protection to the metapopulations of organism in the NW coast of Sweden (approximately 100 % larger metapopulations) than did the OSPAR-network with a high number of MPAs in Swedish Skagerrak. These results suggest that in marine environments where the circulation creates asymmetric connectivities, such as in the Kattegat-Skagerrak area, it can be better to place MPAs outside the area targeted for protection.

Limitations of the study

The present study should be seen as a first test of how modeled data of larval dispersal could be used to assess the effect of larval connectivity for the ecological coherence of MPA networks in the Kattegat-Skagerrak area. The study has several limitations and the results should not be viewed as a blueprint of an optimum design of MPA-networks in the area.

The large spatial scale of the oceanographic model likely leads to an underestimate of the connectivity within a topographically complex coastal zone. Thus, the results indicating very low connectivity within coastal Skagerrak should be interpreted with caution. The poor quality of the data of hard bottom habitats used in the model has likely resulted in a serious overestimate of their distribution, and the analysis regarding connectivity between these habitats should be viewed as an exercise rather than representing true distribution and connectivity. Moreover, the study only assessed the importance of larval connectivity (and indirectly the effect of MPA-size and replication) for the ecological coherence of the MPA-network, and did not include migration of adult stages, neither any aspects of habitat quality nor distribution of species (information that is presently not available). Thus, if other criteria had been included, a different optimal network could have been found.

Still, the oceanographic model is state-of-the-art, and the larval traits simulations are based on a unique set of empirical data providing the best possible assessment to day of larval dispersal and connectivity in the study area. The large-scale dispersal pattern between deeper areas away from the coast does not suffer from the mentioned limitations and therefore provides a better description of the true larval connectivity. Thus, the general results of areas of high and low connectivity and their implications for designs of MPA-networks may be directly of use for managers.

Conclusion

This study provides a demonstration of how oceanographic modeling informed by biological traits of larvae could be used to obtain detailed description of the dispersal and connectivity of larval stages of selected benthic organisms in the Kattegat and Skagerrak region. It also demonstrates how a new theoretical method could be used to identify the optimum MPA-network for different species as well as for whole communities. The results suggest that the present

OSPAR-MPA network in the Kattegat and Skagerrak area does not have the best design in regards of larval connectivity. Most MPAs are too small to allow self-recruitment for the targeted organisms, and they are not placed in the best locations for a functional network. The study suggests that the existing MPA-networks could be improved substantially without increasing their total size, but by carefully selecting the locations that enhance larval connectivity in the network. This would increase the larval supply and population size of the benthic communities, particularly during periods of low abundance, making them more resilient to stressors. While taking the limitations of the study into account, the presented results provide a number of suggestions of how connectivity of the network could be improved by including new MPAs into the network. We find the model methods presented her promising as new tools to assess key criteria for the evaluation of ecological coherence of MPA-networks. We recommend that efforts are made to improve the data on habitat and species distribution in the OSPAR region, which are key for the assessment of MPA-networks.

1. INTRODUCTION

1.1. MARINE PROTECTED AREAS – IMPORTANCE OF LARVAL DISPERSAL AND CONNECTIVITY

The world's marine ecosystems are under severe pressure from habitat destruction, pollution, overfishing and climate change (Halpern et al. 2008). Marine protected areas (MPAs) are considered effective instruments to mitigate the loss of biodiversity and to restore overexploited stocks (Lester et al. 2009). However, resource managers of MPAs face a number of challenges that are rarely a problem in terrestrial systems, where the distribution of habitats and species are generally well known. In contrast, the distribution of marine habitats and species is very poorly documented in the ocean, which is considered a major obstacle for developing functional MPA networks in European waters (HELCOM 2010, OSPAR 2011).

The design of MPAs is further complicated by the fact that most marine organisms have pelagic propagules (e.g. spores, seeds, and larvae; hereafter referred to as larvae) that spend weeks or months drifting in the water column, potentially dispersing large distances (10 to more than 100 km), expanding the scales of connectivity between populations and communities. Most benthic marine organisms therefore form partially open local populations connected in metapopulations through dispersal by planktonic larvae (Caley et al. 1996) where dispersal and connectivity are key factors for local population dynamics and persistence (Cowen et al. 2006). This open population structure has fundamental consequences for the design of marine reserves. For example, the sustainability of local protected populations requires either (1) that reserves are large enough to allow significant self seeding within the reserves (self sustaining), or (2) that protected areas are linked by larval dispersal thereby replenishing one another (network persistence). Thus, in contrast to the designs of terrestrial reserves, which are commonly based on the location of particular habitats and the presence of habitat corridors within a network of reserves (Perault and Lomolino 2000), a marine reserve network should be based on larval dispersal and connectivity between habitats (Gaines et al. 2003, Almany et al. 2009).

However, our knowledge about dispersal distances and connectivity among local marine populations is extremely poor, both because dispersing larvae are minute and difficult to track, and because dispersal is driven by multiple complex factors operating on different spatial scales (Cowen and Sponaugle 2009). This creates serious problems in the design of functional MPA-networks because it is unclear whether a single MPA is large enough to allow significant self-seeding and whether the distances among MPAs (and potential habitats outside the MPAs) isolate or connect meta-populations/communities (Nilsson Jacobi and Jonsson 2011). Moreover, since most MPA-networks aim to protect a large number of different organisms with very different dispersal potentials, the challenge is great to design a network that allows all organisms to persist, if at all possible. Realistic estimates of connectivity between habitats or MPAs that take into account local oceanographic circulation have not been available for any species in the HELCOM-OSPAR region. This lack of information was identified as one major obstacle for evaluating the function of the MPA-networks in Northern Europe (HELCOM 2010, OSPAR 2011, Jonsson et al. 2013).

1.2. LARVAL TRAITS AND DISPERSAL

The transport of larvae among local populations is a complex function of ocean circulation, larval behavior and the duration of the planktonic stage (Shanks 1995). Recent empirical studies have demonstrated that most pelagic larvae are not passively transported during larval development, but show vertical swimming behaviors that lead to species-specific vertical distribution of larvae that may change during larval development or with diel or tidal cycles (Shanks 1995, Queiroga and Blanton 2005). Because the velocity and direction of coastal ocean currents often vary with depth, the vertical position of the larvae may critically affect their dispersal. For example, a recent model study of larval dispersal in the Baltic Sea demonstrated that larval drift depth and duration explained 80 % of the variation in dispersal distance, whereas geographic and annual variation in circulation had only marginal effects (Corell et al. 2012). It is therefore important to include larval behavior and other larval traits (e.g. pelagic larval duration and spawning season) to realistically predict larval dispersal and connectivity. However, our understanding of larval traits and their interactions with oceanographic circulation is very poor, and presently limited to a handful of marine species (Sale and Kritzer 2003, Queiroga and Blanton 2005, Corell et al. 2012). For a large majority of species the larval duration and vertical distribution of larvae is unknown, which poses a serious impediment for understanding larval dispersal and connectivity in marine populations. The effect of larval traits on dispersal has not been included in designs or evaluations of MPA-networks.

1.3. EVALUATION OF CONNECTIVITY IN NORTHEAST ATLANTIC MPA-NETWORKS

In 2003, the OSPAR Commission and the Helsinki Commission (HELCOM) agreed on a joint work program with the aim to establish networks of well-managed MPAs in the Northeast Atlantic and the Baltic Sea, respectively, by 2010. These MPAs, together with *Natura 2000* MPAs should form *ecologically coherent* networks of protected areas (i.e. a network that will allow targeted species and habitats to persist) and assist in preserving biodiversity in the regions (HELCOM 2010, OSPAR 2011).

To evaluate if the networks reach the goals, OSPAR and HELCOM have agreed on 4 main criteria to assess the *ecological coherence* of the networks: (1) *adequacy/viability* (related to size, environmental quality and protection of the MPAs), (2) *representativeness* (regards the inclusion of targeted species, habitats and bioregions) (3) *replication* (regards the number of MPAs within the network with the same features), and (4) *connectivity* (regards the connection between MPAs through dispersal of larvae and adult stages). Among these criteria, connectivity has been considered the most difficult to assess due to lack of information of local circulation and dispersal potential of the targeted species, and because tools to assess larval dispersal and connectivity have been missing. In recent evaluations of the ecological coherence of the OSPAR and HELCOM networks, *connectivity* was only assessed based on distances between sites and on rough estimates of dispersal ranges from the literature (HELCOM 2010, OSPAR 2011, Johnsson et al. 2013).

In the HELCOM evaluation, connectivity was assessed on the basis of theoretical and species-specific fixed connection distances. The theoretical dispersal distances, 25 km and 50 km border-to-border distances between landscape patches, were based on general dispersal estimates in the literature. Four fixed species-specific dispersal distances were also assessed ranging from 1 to 100 km based on genetic and behavioral studies of the species. No attempt was made to include local oceanographic circulation, and the same dispersal distances were applied in all areas (HELCOM 2010).

In OSPARs assessments of connectivity, it is recommended to use 250, 500 and 1000 km as the largest acceptable distance between MPAs in near-shore, offshore and high seas areas, respectively, for the initial assessment of broad scale connectivity (OSPAR 2008). It is not clear what these distances are based on since they are >10x larger than previously recommended maximum distances between MPAs when information is lacking about habitat distribution and larval dispersal (25 km; Halpern et al. 2006, Botsford et al. 2001), and also many times larger than most estimated dispersal distances in the literature (<1 to 200 km; e.g. Shanks et al. 2003, Palumbi 2004, Corell et al. 2012). In OSPAR's most recent evaluation of connectivity in the network, 50 and 80 km was also used as the maximal distance between MPAs in near-shore areas in some regions, based on dispersal distances from the literature. Similar to the HELCOM assessment, no attempt was made to include local oceanographic circulation, and the same dispersal distances were applied in all areas (Jonsson et al. 2013). The lack of information and tools to properly assess the connectivity was identified as one major obstacle for a proper evaluation the ecological coherence of the OSPAR and HELCOM MPA-networks (HELCOM 2010, OSPAR 2011, Johnsson et al. 2013).

The theoretical dispersal distances used in published assessments are to a large extent based on estimates from the open coasts of northwest America where a general relationship has been found between the length of the pelagic larval stage and their dispersal distance (Shanks et al. 2003). However, recent studies show that dispersal distances based on the duration of the pelagic larval stage can be over-simplistic. Local oceanographic features and behavioral mechanisms can result in unexpectedly high local recruitment (self-seeding) (e.g. Cowen et al. 2000, Sotka et al. 2004).

Because larval dispersal can be strongly affected by local oceanographic conditions, dispersal and connectivity of species targeted by a marine reserve should be assessed in a local context. The transport of water in the Kattegat-Skagerrak area is quite unique because of the weak tidal influence, the baroclinic estuarine circulation, and the large effect of meteorological wind events (Rodhe 1998). Moreover, care should also be taken regarding the use of data on larval traits from other areas, particularly if the environmental conditions differ. For example, shore crab larvae (*Carcinus maenas*) from the British Isles display an inherited vertical migration behavior in phase with local tides that affect their horizontal transport, whereas shore crab larvae in the Skagerrak area display a nocturnal vertical migration behavior (Queiroga et al. 2002). Thus, region-specific factors must be taken into account when assessing larval dispersal and connectivity of MPAs in an area.

1.4. ASSESSING LARVAL DISPERSAL AND CONNECTIVITY WITH BIOPHYSICAL MODELS

Optimal design of spatial conservation strategies for marine species would require a complete description of larval dispersal for all target species over many years. Ideally, this would consist of dispersal trajectories for all successful settlers in a metapopulation presented in a connectivity matrix that reflects how many larvae from a set of origins settle successfully at a set of destinations (Largier 2003). However, since it is not possible to obtain such direct and comprehensive observations of dispersal in nature, information of dispersal has to rely on indirect measures with various levels of interpretation.

One of the most promising alternative methods to assess larval connectivity is numerical modeling of larval dispersal using 3D-hydrodynamic models of oceanographic flow coupled with models of biological traits (e.g. spawning season, larval duration and swimming depth). Assessments of such biophysical models have shown that they can successfully predict larval dispersal and connectivities in e.g. fish (Cowen et al. 2006, van der Molen et al. 2007). This approach has the advantage that it can generate a very high number of dispersal trajectories with high coverage in space and time resulting in detailed connectivity matrices for a range of dispersal strategies. Recently biophysical models have also been applied in a few studies to assess how dispersal and connectivity affect the designs of MPA-networks (White et al. 2010, Moffitt et al. 2011, Corell et al. 2012).

Although these models can produce detailed connectivity matrices between sites, methods have been lacking of how to use the resulting connectivity matrices, which describe dispersal probabilities among sites, in a process to select an optimal network of MPAs. However, in a recent theoretical study, Nilsson Jacobi and Jonsson (2011) applied *eigenvalue perturbation theory*

(EPT) on a connectivity matrix to identify the most valuable local populations for a metapopulation, and demonstrated that the EPT-method could be used as a tool to find optimal MPA networks. With this new method it is also possible to compare the relative effects of connectivity and habitat quality for population persistence (Berglund et al. 2012). However, so far the EPT-method has only been applied on single-species connectivity matrices, and has not been applied to realistic assessment of existing MPAs. In the present study we assess its use in the Kattegat-Skagerrak region for finding optimal MPA-networks for a community of species with different life histories, dispersal strategies and connectivities.

1.5. AIMS OF STUDY

The overall aim of this study is to describe the larval dispersal and connectivity of benthic organisms in the Kattegat-Skagerrak area of the North Sea to evaluate the effect of larval connectivity on network persistence, contributing to ecological coherence, within the MPAs in the area, with special focus on the OSPAR-MPAs. This was achieved in 4 steps: First, a library of larval traits of species found in the Kattegat-Skagerrak area was created by compiling a large empirical data set available in the research group and reviewing the literature. Special attention was given to OSPAR's list of threatened and/or declining species and habitats. This database was then used to create realistic larval-types that represent selected species groups of the targeted benthic communities in the model study. Second, the dispersal of these larval-types was simulated in a biophysical model to generate detailed connectivity matrices for both individual larval types and communities between different habitats and between MPAs. Third, the EPT-method was used to identify the most valuable sites for individual metapopulations and metacommunities in the study area, and these optimal networks were compared to the existing MPA-networks. In a last step, the metapopulation size expected from protection through an EPT-selected network was compared to the metapopulation size expected from protection within the existing MPA-networks, using simple population models, to evaluate the effect of larval connectivity on the different networks.

2. LARVAL TRAITS OF MARINE FISH AND INVERTEBRATES IN THE KATTEGAT-SKAGERRAK REGION

2.1 METHODS

Since almost no information exist in the literature regarding larval traits (vertical distribution, pelagic larval duration and spawning season) from the Kattegat-Skagerrak area, empirical data from different plankton surveys, available in the research group, was compiled to create a library of larval traits for benthic fish and invertebrate species from this area. This information could then be used to parameterize the biophysical model and create more realistic virtual larval-types that would represent selected species groups of the targeted benthic communities in the model study. The empirical data was complemented with a literature search to find information of pelagic larval duration (PLD), which was not obtained from the plankton survey, and to complement the information of the spawning season (periods when larvae are present in the water). Since one specific aim of study was to assess connectivity between OSPAR-MPAs, a special database of larval traits was created for the species in OSPAR's *list of threatened and/or declining species and habitats* that are regularly found in the study area.

2.1.1 Larval sampling surveys

Single net samples

Most of the depth-specific larval data was collected using an opening and closing circular plankton net (250 µm mesh, 0.5 m^2 opening) that were fished in the Gullmarsfjord (N58°16', E11°28'), or just offshore the Gullmarsfjord area (N58°16', E11°20'), on the Swedish northwest coast in eastern Skagerrak during summer months (when most species have larvae in the water) 2005–2007. In 2007, a plankton survey over a larger area in Skagerrak and Kattegat was also carried out where 8 stations were sampled from the Gullmarsfjord to north of Danish Skagen (N57°50', E10°35'), and Läsö (N57°20', E10°45') to west of Gothenburg (N57°42', E11°34') on the Swedish west coast. In all surveys, replicate samples from above and below the pycnocline were taken (2–5 specific depths per survey), and sampling was carried out both during day and night conditions (see Table 1 for details). In total, 248 separate plankton samples were included in the analysis.

The depth-specific samples were collected by lowering the plankton net to target depth and opening it using a mechanical double release mechanism. The net was subsequently towed at approximately 2 knots for 5 min before it was closed and retrieved to the boat. The sampling depth, salinity and temperature during the sampling were monitored using a hand-held CTD attached 1.5 m below the plankton net. The sampled depth was ±2 m of the targeted depth in all samples. For the surface samples, two buoys were attached to the top of the plankton net so that the top of the net just broke the surface when it was towed, fishing the top 0.7 m of the water surface. The plankton net was fitted with a mechanical flow meter to estimate the volume sampled.

Table 1. Summary of plankton surveys included in the study from with data of larval drift depth and season were obtained. The table shows the total number of samples, the number of sites, depths, and dates sampled in each survey, and the months and years the samples were collected. See text for more information about the sites.

Sample area	Tot. no. samples	No. sites	No. depths	No. dates	Months	Years
Gullmarsjord	70	1	3-5	4	Jul-Aug	2005-2006
Gullmarsjord area	48	3	2	4	Jul-Aug	2005-2006
Gullmarsjord area	66	1	4	5	Jul-Aug	2007
Skagerrak-Kattegat	64	8	2	4	Jul	2007
Skagerrak-Kattegat	82	2	5	13	Jan-Dec	2009-2010

Multinet samples

To obtain better data of the spawning season in Skagerrak and Kattegat samples from an extensive plankton survey were also analyzed. The survey, carried out in collaboration with the EU-project BAZOOCA (Baltic zooplankton cascades) and the Swedish Meteorological and Hydrological Institute (SMHI), consisted of 13 separate 5-day cruises from May 11, 2009 to April 16, 2010. In the present study, data from one station in the Gullmarsfjord and one station in southern Kattegat (Anholt; (N56°41', E11°46') where 4 and 3 depth-specific samples from 35 m to the surface were collected, respectively. The plankton samples were taken with a multinet plankton sampler (Hydro-bios) with a 0.5x0.5 m opening fitted with 5 separate nets equipped with 300 µm mesh. Samples were taken at all hours of the day (see Table 1 for details). In total, 80 separate plankton samples were included in the analysis.

Analyses

All samples were immediately fixed in ethanol or formaldehyde, before identification and measurement under a stereomicroscope in the laboratory. Experts at the Institute of Marine Research – Lysekil, Swedish University of Agricultural Sciences, carried out all identifications of fish larvae. Invertebrate larvae and stages were identified at the department of Marine Ecology, University of Gothenburg following the descriptions given by Enckells (1980), Ingle (1992), and Young (2002). All counts were standardized to number of larvae 100 m^{-3}. Not all larval species and stages were analyzed in all samples and the number of replicates per species-stage varied between 132 and 330.

For each larval species-stage we estimated: the number replicates (n), the number of samples where the species/stage occurred (N), the average density (+SE), the proportion of larvae located at 0–10 m depth (above the pycnocline) day and nigh, the proportion of larvae located at 20–30 m depth (below the pycnocline) day and nigh, the proportion of the larvae located at 0–10 m depth (compared to deeper) during the day, the proportion of the larvae located at 0–10 m depth during the night, the larval occurrence (months when larval species/stage occurred at least once in the samples), and the larval peak (months when the highest densities occurred). We also plotted the overall average depth distribution, and the average depth distribution from day and night samples, and the average density per month for all identified taxa in separate graphs. In the analyses of differences between day and night, data collected at twilight (±2 h around sunset and sunrise) were excluded from the analyses. Since the twilight data were included in the analyses of overall depth distribution these result may differ from the day-night results.

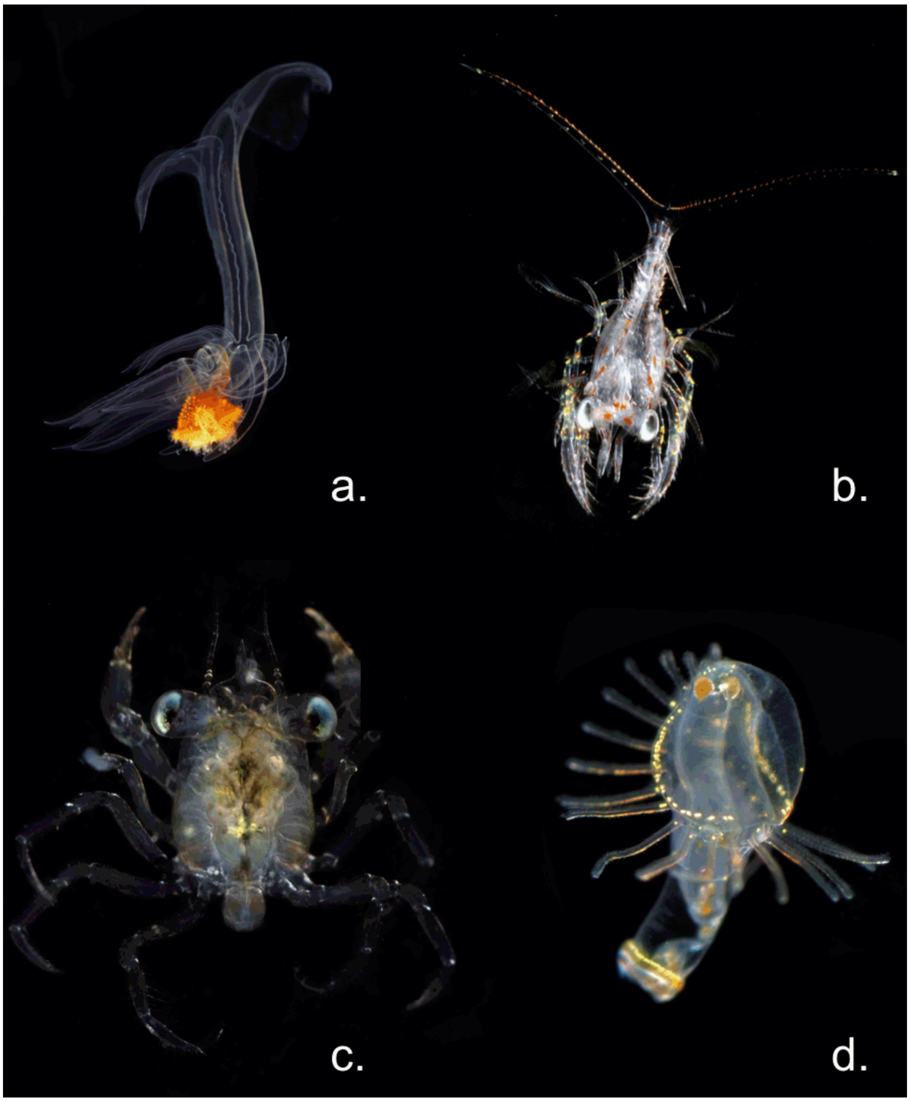


Figure 1. Examples of larvae collected in the plankton survey. Larva of (a) the sea star Luidia sarsi, (b) the Norwegian lobster Nephrops norwegicus, (c) the swimming crab Liocarcinus sp., and (d) the horseshoe worm Phoronis mulleri (cf.). Photos Erik Selander.

2.1.2 Literature survey

The empirical data from the plankton surveys were complemented with a literature search to find information of pelagic larval duration (PLD), which was not obtained from the plankton survey, and additional information of the spawning season (periods when larvae are present in the water), and drift depth for taxa that were not collected in the plankton surveys. The search also targeted the species in OSPAR's *list of threatened and/or declining species and habitats* that are regularly found in the study area (OSPAR 2008). We started the search in the scientific literature using Thomson Reuters Web of Knowledge database, and Google Scholar. Since there is a general lack of information of larval traits in the literature, information was also searched for on the scientific websites *World Register of Marine Species* (WoRMS) and *Marine Life Information Network UK* (MarLIN). The aim was always to find information about the larval traits for the target species and from the study area. If that failed both the geographic region and the taxonomic breath was extended until information was found. For some phyla with small and hard to identify larval stages, e.g. cnidarians, sponges (Porifera), most molluscs and polychaetes, etc., particularly for deep living taxa, very little information was found, and the larval traits were often based on information on a phylum level.

2.2 RESULTS

A total of 80 taxa and stages of invertebrate larvae and 45 taxa of fish larvae were collected and identified (see Fig. 1 for examples of taxa collected). Most taxa showed a non-random depth distribution where the larvae were concentrated at a specific depth-strata. Most larvae were also present in the water during a distinct period of the year (see Fig. 2ab for examples). Although the distribution showed clear species-specific patterns, there was large variation in depth distribution within taxa at any sampling time, demonstrating a variation in behavior within taxa. See appendix C for graphs of the vertical distribution and seasonality of larvae, and Table A1.1 and A1.2 (Appendix A) for a summary of the results of all invertebrate and fish larvae, respectively.

2.2.1 Depth distribution and seasonality of invertebrate larvae

Larval stages from a total of 80 taxa were identified. For 25 taxa the occurrence (i.e. the number of samples where the taxa were encountered) was <10, and these have not been included when summarizing the results below (unless belonging to taxa listed by OSPAR). For the remaining 65 taxa, the occurrence was >100 in many cases, providing a good database to assess the vertical distribution of larvae in the Kattegat-Skagerrak area.

Most larval taxa were concentrated below the pycnocline at 10–50 m depth; for many taxa 85–100 % of the larvae were found at depths ≥20 m (e.g. bivalves, cnidarians, several taxa of echinoderms, polychaetes, and crustaceans). Only larvae of polychaete scale worms (Polynoidae), bryozoa, one group of sea stars (Asteroidea), grass and sand shrimp, and the two species of swimming crabs had a majority of larvae (54–85 %) swimming in 0–10 m depth. Only phoronid larvae had similar densities at all depths (Table A1.1, appendix A).

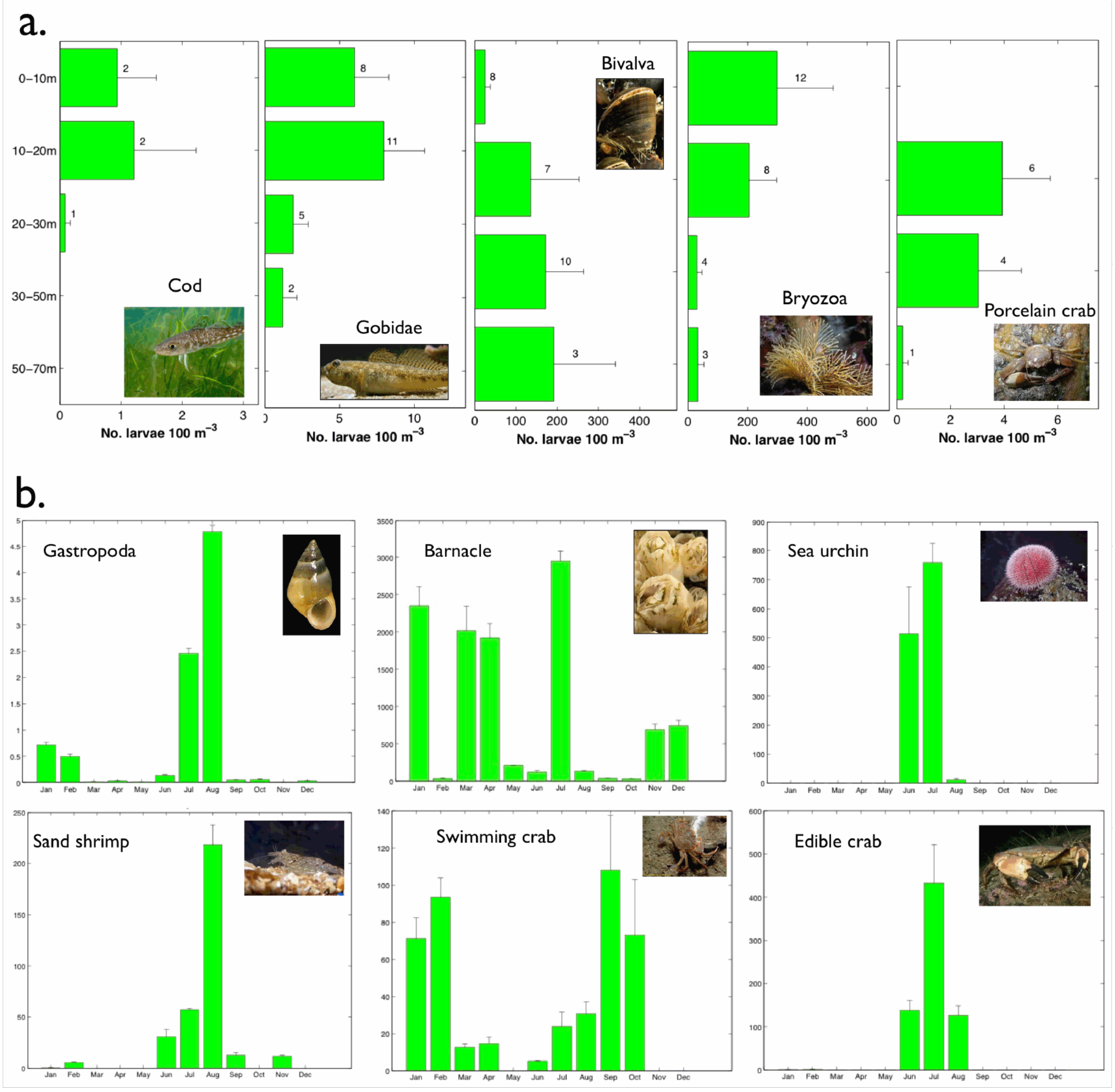


*Figure 2. Examples of results from the plankton survey. (a) Average larval depth distribution of cod (*Gadus morhua*), gobid fish, mussel (bivalve), moss animal (bryozoa) and the long-clawed porcelain crab (*Pisidia longicornis*). (b) Average larval abundance per month for gastropod snails, barnacles, sea urchins, the sand shimp* Crangon crangon*, the swimming crab* Liocarcinus sp.*, and the edible crab* Cancer pagurus*. For all results see appendix C.*

Among the taxa where sample size was sufficiently large, nocturnal vertical migration behavior was only indicated in a few taxa, i.e. in the trochophore stage of polychaetes, brittlestars, the squat lobsters *Munidopsis* sp. and among some portunid crabs (see below for details). In grass shrimp (*Palaemon* sp.) and sand shrimp (*Crangon* sp.) that live in shallow coastal habitats as adults, the proportion of larvae that swam above the pycnocline increased from below 10 % in early larval stages to 43–80 % in late larval stages, indicating an ontogenetic change in larval behavior. In the two deep-living crab species (*Corystes cassivelaunus* and *Atelecystus rotundatus*) the opposite pattern was observed where the proportion of larvae that swam above the pycnocline decreased from 27–57 % in early larval stages to zero in postlarval stages. No other clear indication of changes in larval swimming depths during larval development was found (Table A1.1, appendix A).

Most taxa showed a distinct spawning season during the summer with peak densities in June to August (e.g. bivalves, gastropods, most echinoderms and crustaceans). Among these, e.g. gastropods, Norwegian lobster, a species of portunid crabs, and several anomuran crabs showed an extended spawning season from March to October. Larvae of the sea star *Ludia sarsi* showed the opposite pattern and was not encountered during the summer months, but showed high densities from October to April. Nudibranchs and phoronid larvae were only present in the fall from August to December, whereas bryozoans, spionid polychaetes were present in the water at all months of the year with peak densities during winter months. Barnacle larvae were present in high densities year around with no clear peak (Table A1.1, appendix A).

Below we have summarized the main results phylum by phylum for the well-sampled taxa. The referenced plates are all found in appendix C on the indicated pages.

Mollusca

The mollusc-larvae could only be separated into bivalves (e.g. mussels, oysters) and gastropods (e.g. sea snails). Bivalve veliger larvae were found at all depths, but were concentrated below the pycnocline (91 %) at 20–30 m. Bivalve larvae were only collected during the summer months, with a clear peak in July (plate 1, 81).

Gastropod veliger larvae showed a less distinct depth distribution with highest densities at 5–25 m, and were collected from April to December, although densities peaked in July and August. Larvae or pelagic stages of juvenile nudibranchs (c.f. Nudibranchia) had similar densities above and below the pycnocline and a spawning season later in the fall (July to December; plate 2–3, 82–83).

Polychaeta

Four types of polychaete-larvae were identified that showed different vertical distributions. Polychaete trochophore larvae displayed a nocturnal vertical migration, with higher densities below the pycnocline at 30–50 m depth during the day, and higher densities at the surface during the night (plate 4). Among the later larval stages that could be identified to family, spionids were concentrated below the pycnocline at all times (72–100 %), whereas polynoids (scale worms) were also found in high densities above and often close to the surface. Spionid larvae were found year around but with a clear peak in January to April, whereas polynoids were present from March to July (plate 4–7, 84–87).

Phoronida

Larvae of the small phylum Phoronida (horseshoe worms; Fig. 1d) were evenly distributed between 0–50 m depth at low densities, with a distinct spawning season in the fall (August to December; plate 8, 88).

Bryozoa

Bryozoan (moss animals) cyphonautes larva were concentrated from 0–20 m (97 %), with a majority above the pycnocline, and distinct spawning season in the winter with highest densities from December to March (plate 9, 89).

Cnidaria

The small planula larvae of cnidarians (e.g. hydrozoans, jelly-fish, sea anemones, sea pens) were not adequately sampled in the plankton survey and are very difficult to identify, even to taxonomic class. Only a few planula larvae were collected in March and April, which were found below the pycnocline (plate 10, 90).

Echinodermata

Among echinoderms, the pluteus larva and juvenile stages of brittle stars (Ophiuroidea) and sea urchins (Echinoidea) were predominantly found below the pycnocline (61–99 %). However, in all larval stages, larvae displayed a nocturnal vertical migration behavior resulting in higher densities of larvae in surface waters at night than during the day. The larvae showed a distinct peak in abundance during June and July (plate 12–14, 91–93).

For sea star larvae (Asteroidea), the depth distribution varied between larval stage and groups. The bipinnaria larvae (the first larval stage of most sea stars) were predominantly found above the pycnocline (78 %), whereas the later brachiolaria stage was also common at greater depths; the larval abundance peaked in June and July (plate 15–16, 94–95). In contrast, the conspicuous larvae of the sea star *Luidia sarsi* (Fig. 1a) were only collected from fall to spring, and the larvae were concentrated below the pycnocline (90 %; plate 17, 96).

Crustacea

Larval stages of crustaceans are relatively large and, in comparison to other invertebrates, relatively easy to identify to species and development stage. A total of 63 taxa and larval stages of crustaceans were identified that showed a large variation in vertical swimming behavior and spawning season.

Larvae of cirripeds (barnacles, goose barnacles and some parasites) were found in high densities at all depths, where nauplius larvae were more concentrated around the pycnocline at 10–20 m depth, and the last larval stage (cyprid stage) were most abundant at 20–30 m depth, but also showed high concentrations at the surface. Cirriped larvae were found in the water all year around with highest densities from January to July (plate 18–19, 98–99).

Among shrimp larvae (Caridea), the vertical distribution of grass and sand shrimp (*Palaemon* spp. and *Crangon* spp., respectively) indicated an ontogenetic shift where early zoeal stages had a distribution mainly below the pycnocline (92 %), and later stages were mainly found at 0–10 m depth (43–80 %), particularly at night. These larvae were abundant mainly from June to August (plate 21–26, 100–101).

Larvae of the mud or ghost shrimp *Callianassa* sp., of which *C. subterranea* is listed by OSPAR (Table A1.3, Appendix A), were found mainly below the pycnocline (90 %) at 10–50 m depth, from July to August (plate 33, 108). The mud shrimp *Calocaris macandrea* is also listed by OSPAR, and larvae of *Calocaris* spp. had highest abundance at 5 m depth, although 56 % of the larvae were still below the pycnocline on average (plate 36, 110).

Similarly, larvae of the burrowing mud shrimp *Upogebia* spp the Norwegian lobster (*Nephrops norvegicus*; Fig. 1b), pagurid hermit crabs, squat lobsters (*Galathea* spp.) and long-clawed porcelain crab (*Pisidia longicornis*) were mainly found below the pycnocline (70–95 %; plate 34–35,37–38, 41–43, 45–46). However, post-larvae of the squat lobsters *Munidopsis* spp. displayed a nocturnal vertical migration behavior resulting in highest densities of larvae in surface during the night (plate 44). All species showed a peak in larval abundance from June to August, where larvae of hermit crabs and Norwegian lobster also were abundant in March to May (plate 109, 111, 113–116).

Among the large and abundant group of brachiuran crabs, a nocturnal vertical migration behavior of variable strength was indicated in several species of portunid crabs (swimming crabs: e.g. the shore crab *Carcinus maenas*, the velvet swimming crab *Necora puber*), resulting in higher densities of larvae in surface waters at night than during the day. However, a majority of all larvae were still found below the pycnocline on average (plate 47–61). One exception was the small swimming crab *Liocarcinus* cf. *navigator*, where a majority of the late stage larvae swam at the surface, particularly at night (67–100 %). Larval stages of the edible crab *Cancer pagurus* were also mainly found below the pycnocline (64–81 %), with a few individuals migrating to the surface at night (plate 62–63). All portunid crabs and the edible crab showed a peak in larval abundance from June to August, where *L. navigator* differed from the other species in showing a more extended spawning season from March to October (plate 117–123).

A few larvae were collected of the crab species *Thia scutella*, *Corystes cassivelaunus* and *Atelecystus rotundatus*, which are listed by OSPAR (Table A1.3, Appendix A). A majority of the larvae for all three species were found below the pycnocline, but for *C. cassivelaunus* and *A. rotundatus* early stage zoea larvae were found also in surface waters (27–57 %), whereas the post-larval (megalopae) stage was only found below the pycocline at 25–50 m depth. *T. scutella* and *C. cassivelaunus* were collected from March to August, whereas *A. rotundatus* was only found in July an August (plate 64–70, 124–126).

2.2.2 Depth distribution and seasonality of fish larvae

A total of 45 taxa of fish larvae were identified, but for 29 taxa the occurrence was <10, and 8 taxa were only encountered once. Thus, in comparison with invertebrates, the data on fish larvae is limited, and the summary below is focused on the 16 taxa with a higher occurrence of larvae.

Most species of the collected fish larvae showed higher concentrations below the pycnocline at 10–50 m depth. However, herring larvae, most gadoid, labrid and gobid larvae, and several species of flatfish and cottid larvae showed high concentrations above the pycnocline (30–100 %). In contrast to the invertebrates, there was little indication of nocturnal vertical migration among the fish larvae, and no clear indication of shifts in vertical distribution during development. Similar to invertebrates, most fish larvae were encountered during the summer months with peak densities in June to August. The exceptions were herring, gadoid and most pleuronectid flatfishes that had higher densities in the spring. Only one species, the sand eel *Ammodytes lancea* was present all months of the year (Table A1.2, Appendix A).

Clupeiformes

Herring larvae (Clupeidae) were collected from all depths (0–50 m), with higher densities at 0–30 m. The younger larvae L <10 mm were found at high densities mainly at 0–20 m depth, with 38 % above the pycnocline, whereas older larvae showed a slightly deeper distribution with high densities also at 20–30 m, and only 28 % above the pycnocline. Herring larvae peaked in abundance in March and April but were present in the samples until August (plate 135–137, 181).

Gadiformes

Cod (*Gadus morhua*) is on OSPAR's list of threatened and/or declining species (OSPAR 2008) and cod larvae were encountered in 5 samples in March and April at relatively high abundance (6.8 larvae 100 m^{-3}), concentrated around and above the pycnocline (0–20 m), with 39 % above the pycnocline. Larvae of the four-beard rockling (*Enchelyopus cimbrius*), were collected in high numbers from June to November at 0–20 m depth with 51 % above the pycnocline. Larvae of whiting (*Merlangius merlangus*) and unidentified larvae of the Phycidae family were also caught occasionally, which also showed high abundance in surface water. In contrast, larvae of tadpole fish (*Raniceps raninus*) and herring hake (*Merluccius merluccius*), which were only caught on one occasion, were found below the pycnocline (plate 138–143, 182–187).

Perciformes

Most of the perciform larvae were collected during the summer months with a peak in June to August. The sand eel *Ammodytes lancea* was an exception with larvae present from January to December. Gobid larvae also had an extended spawning season with low densities also in the spring (plate 188–202). Among the species with a better sample size, many were concentrated at 0–20 m depth with a substantial proportion above the pycnocline (on average 30–62 %; e.g. goldsinny wrasse *Ctenolabrus rupestris,* corkwing wrasse *Symphodus* cf. *melops*, sand eel, gobidae larvae, and weever *Trachinus* sp.). The weewer was the only fish species where larvae displayed an indication of nocturnal vertical migration (plate 158). Other taxa were concentrated mainly below the pycnocline (on average >80 %), e.g. larvae of the dragonet *Callionymus* sp., the Carangidae family and others (plate 144–158).

Pleuronectides

The larvae of flatfishes could be divided into a group with larvae present in the spring and early summer (e.g. common dab *Limanda limanda*, flounder *Platichtys flesus* American plaice *Hippoglossoides platessoides*) and those with larvae only during the summer (Mediterranean scaldfish *Arnoglossus laterna*, common sole *Solea* cf. *sole*, and Solenette *Buglossidium luteum*; plate 203–214). Larvae of most species were concentrated below the pycnocline (80–100 %; including Scophtalmidae larvae), but 4 species (A. *laterna, H. platessoides, P. flesus* and *S. solea*) were found at high concentrations (31–86 %) also close to the surface (plate 159–171).

Scorpaeniformes

Larvae of the order Scorpaeniformes were collected from April to September, but showed low occurrence, making it difficult to draw conclusions about their vertical distribution. Cottid larvae were found mainly above the pycnocline whereas larvae of the grey gurnard *Eutriglia gurnardus*, snailfish *Liparis* sp. and lumpfish *Cyclopterus lumpus Liparis* were only caught below the pycnocline (plate 215–219, 172–176).

Syngnathiformes

Three species of young juvenile pipefish (*Entelurus aequoreus Nerophis* sp. *Syngnathus* sp.) were collected in July and August at low occurrence, which were all concentrated above the pycnocline (63–100 %; plate 220–222, 177–179).

2.2.3. Larval traits for OSPAR's list of threatened species

In collaboration with managers of MPAs at the County Administrative Board of Västra Götaland, Sweden, 43 benthic organisms were identified from OSPAR's list of threatened and/or declining species that are commonly found the Kattegat-Skagerrak region (Table A1.3, Appendix A). For most species, very little species-specific information of larval traits was found in the literature, and larvae for only 5 of the listed species were collected in the plankton survey (all decapod crustaceans; see 2.2.1). However, for most phyla, the plankton survey provided information on drift depth and spawning season for related species, and similarly we found information in the literature about pelagic larval duration (PLD) for related species for most taxa, sponges and antozoans being exceptions (Table A1.3, Appendix A).

The lack of information for benthic sponges (Porifera) and anthozoans (Cnidaria; e.g sea anemones, sea pens, and corals) that form critical habitats for a large number of species on both soft and hard bottoms in the study area, are likely related to the fact the they have small larvae with a simple morphology making them difficult to identify and there are few published descriptions. According to laboratory studies found in the literature, most species have a short larval duration, which likely explains the low number of collected larvae in the plankton survey, and the lack of information of larval drift depth in the literature. Although little data was obtained regarding the larval traits for these groups, the very short PLD suggested in the literature (<3 d) for the sponges, the corals from the Pleuxauridae and Clavulariidae families, and the hydrozoa *Nemertesia spp.* (Table A1.3, Appendix A) suggest that the larvae likely stay close to the benthic habitat and are dispersed short distances (<1 km), resulting in local recruitment. Since the model study assessed dispersal on a scale >3.7 km, these species were not represented in the connectivity study. However for the remaining species, information of drift depth, PLD and spawning season were obtained for at least related species allow approximation of their dispersal in the model study.

3. BIOPHYSICAL MODEL STUDY OF LARVAL CONNECTIVITY AND ECOLOGICAL COHERENCE OF MPAS

To describe the larval dispersal and connectivity of benthic organisms in the Kattegat-Skagerrak area of the North Sea, a biophysical model study was carried out using a 3-D ocean circulation model coupled with a particle-tracking model. Based on the resulting larval connectivity, we identified the optimal network of sites that maximises metapopulation persistence. These areas were finally compared with existing MPA-networks to assess the ecological coherence of the existing and the optimal networks.

3.1 STUDY REGION

The biophysical model-study was carried out in the Skagerrak-Kattegat area of the North Sea. This area borders the Baltic Sea and is strongly influenced by the outflow of brackish water through the Danish straits (Öresund, Great Belt and Little Belt) into the Kattegat, resulting in a strong halocline at approximately 10–15 m depth, and a gradient of surface salinity from approximately 10 in the Danish straits and southern part of Kattegat to 34 in northern Skagerrak. The Baltic current, which brings low saline surface waters from the Baltic Sea northward along the Swedish west coast, is the main residual component of the flow through Kattegat, but can be temporarily reversed on occasions with strong westerly winds. The Baltic current continues out in Skagerrak where the strong and permanent Norwegian coastal current, with velocities ranging up to 150 cm s^{-1}, continues the transport of the Baltic Sea outflow to the Norwegian Sea (Fonselius 1996). The dominant coastal current in the southeastern North Sea is the Jutland current, which transports North Sea water along the west coast of Jutland and into Skagerrak and Kattegat, where it meets the Baltic current and turns north. Tides in Skagerrak and Kattegat do not play an important role for the water circulation, which is determined mainly by baroclinic flow of Baltic water and wind forced currents (Andersson and Rydberg 1993, Rodhe 1998).

3.2 METHODS

3.2.1 Biophysical model

To explore the dispersal of planktonic larvae in the simulation experiment, two different computer models were used. First a 3-D ocean circulation model produced fields of velocity, density, salinity and temperature to describe the environment in all parts of the model domain for the modelled time period. Secondly, a particle-tracking Lagrangian trajectory model calculated the displacement of individual virtual larvae (trajectories) in the flow field. Based on empirical data on larval traits, we assessed the dispersal and connectivity of 14 different virtual larval types representing selected groups of benthic organisms found in the study area. Using the resulting connectivity matrices, and applying the *eigenvalue perturbation theory* (EPT)-method, we identified optimal networks of protected sites for individual metapopulations and metacommunities in the study area. These networks were finally compared with existing MPA-networks using simple metapopulation models to assess the ecological coherence of the existing and the optimal networks.

3.2.1.1 Oceanographic model

The ocean flow data used for the model study were produced with the BaltiX model, which is a regional Baltic/North Sea configuration of the NEMO ocean model (Madec 2010; http://www.nemoocean.eu/). The spatial resolution is 2 nautical miles (3.7 km) in the horizontal, and 56 levels in the vertical, ranging from 2 m intervals at the surface to 22 m in the deepest parts. The model has a free surface and allows the grid boxes to stretch and shrink vertically to accurately model the tides without generating empty grid cells at low tide. The computational domain of BaltiX covers the entire Baltic Sea, the North Sea and English Channel, with open boundary conditions between Cornwall and Brittany, and between the Hebrides Islands and Norway. A regional atmospheric model (Rossby Centre regional atmospheric model) with a resolution of 50 km is used for the atmospheric forcing. The model has been validated and shown to provide realistic sea surface height (SSH), sea surface temperature (SST), ice cover, and deep-water salinity (Hordoir et al. 2013a). The water exchange between the Baltic and the Kattegat in the BaltiX model is analyzed in Hordoir et al. (2013b).

3.2.1.2 Particle tracking model

The dispersal of virtual larvae was calculated with the Lagrangian trajectory model TRACMASS (Döös 1995, De Vries and Döös 2001). It is an off-line particle-tracking model that calculates transport of particles using flow field data from a 3-D circulation model. Velocity fields were updated for all grid boxes in the model domain every three hours in this study, and the trajectory calculations were done with a 15-minute time step. To get the trajectory of a given particle the velocities are interpolated from the sides of the grid box and the successive transportation of the particle within the box is calculated analytically. To mimic larval traits, the vertical position of the trajectories was locked at predetermined depths. For a technical /mathematical description of the algorithms used in TRACMASS see for example the appendix in Döös (1995), and de Vries and Döös (2001).

3.2.1.3 Study domain, habitat distribution and larval types

Study domain

In the model experiment, larval trajectories were released and monitored for settlement in all 3.7x3.7 km model grid cells from 1–100 m depth in an area starting in the German Wadden Sea in the west to the western part of the Baltic Sea in the east (Fig. 3). The study area consisted of 8 992 grid cells. Although the focus of this study was only on the Kattegat-Skagerrak area, a larger region was included in the model to avoid boundary effects and to allow a natural exchange of larvae also from nearby regions. To assess connectivity between different parts of the Kattegat-Skagerrak area, it was divided into 5 separate regions (1) western Kattegat, (2) eastern Kattegat (including the Öresund strait), (3) eastern Skagerrak (the Swedish northwest coast), (4) western Skagerrak (north of Danish Jutland), and (5) northern Skagerrak (the south coast of Norway). Since bottoms deeper than 100 m was not included in the assessment of larval dispersal, the connectivity of the deeper central part of Skagerrak was not assessed (Fig. 3). The dispersal experiments were repeated for 8 years (1995–2002) to cover extremes in the North-Atlantic Oscillation cycle (Hurrell and Deser 2009).

Habitat distribution - BALANCE data of hard substrate

To accurately model connectivity between organisms it is critical to have information about their distribution in space. However, data is lacking on the distribution of almost all marine species and biotic habitats in European waters, which is considered the major obstacle for developing functional MPA-networks (HELCOM 2010, OSPAR 2011). To assess the effect of including habitat restrictions on the spatial distribution of benthic organisms we made an attempt to use modeled data of the distribution of hard substrate in the study area, developed within the EU-project BALANCE (Leth et al. 2008) and EUSeaMap (Cameron and Askew 2011). The habitat data were obtained as polygons in GIS layers (shape files). The habitat polygons were sampled with a dense grid (1 x 1 km^2) and all grid points falling within the BaltiX grid cells were queried for habitat type. If any sample point within a BaltiX grid cell indicated hard substrate this grid cell was considered to harbor hard substrate habitats. The hard bottom substrates were separated into shallow (1–20 m) and deep (21–100 m) hard bottom habitats (Fig. 4).

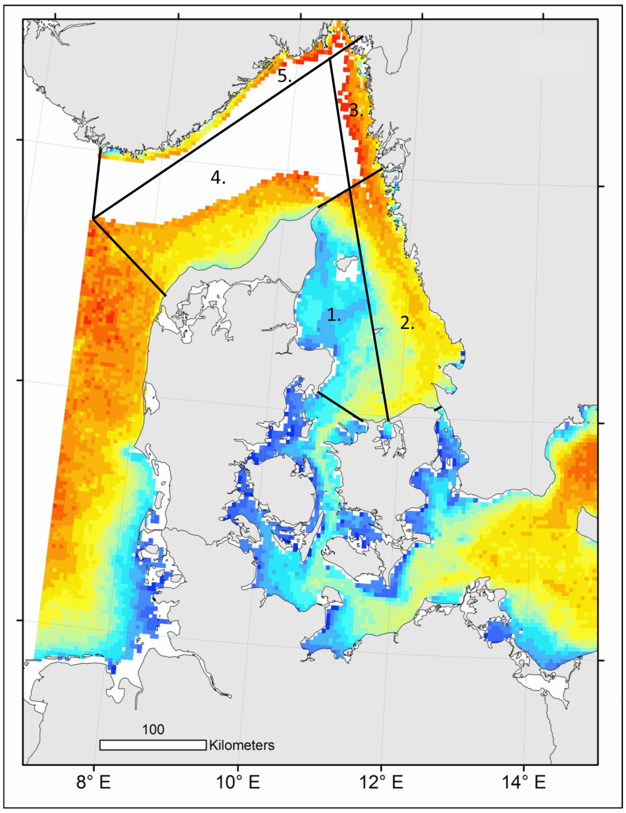


Figure 3. Map showing the model domain (colored area) and the study area separated into 5 regions (1) western Kattegat, (2) eastern Kattegat, (3) eastern Skagerrak (the Swedish NW coast), (4) western Skagerrak (north of Danish Jutland), and (5) northern Skagerrak (the south coast of Norway). Since bottoms deeper than 100 m was not included in the assessment of larval dispersal, the connectivity of the deeper central part of Skagerrak was not assessed (white area in Skagerrak on map). The Danish Straits (Öresund, Great Belt and Little Belt) were also included in the study, though not assessed as separate regions in the source-sink analyses.

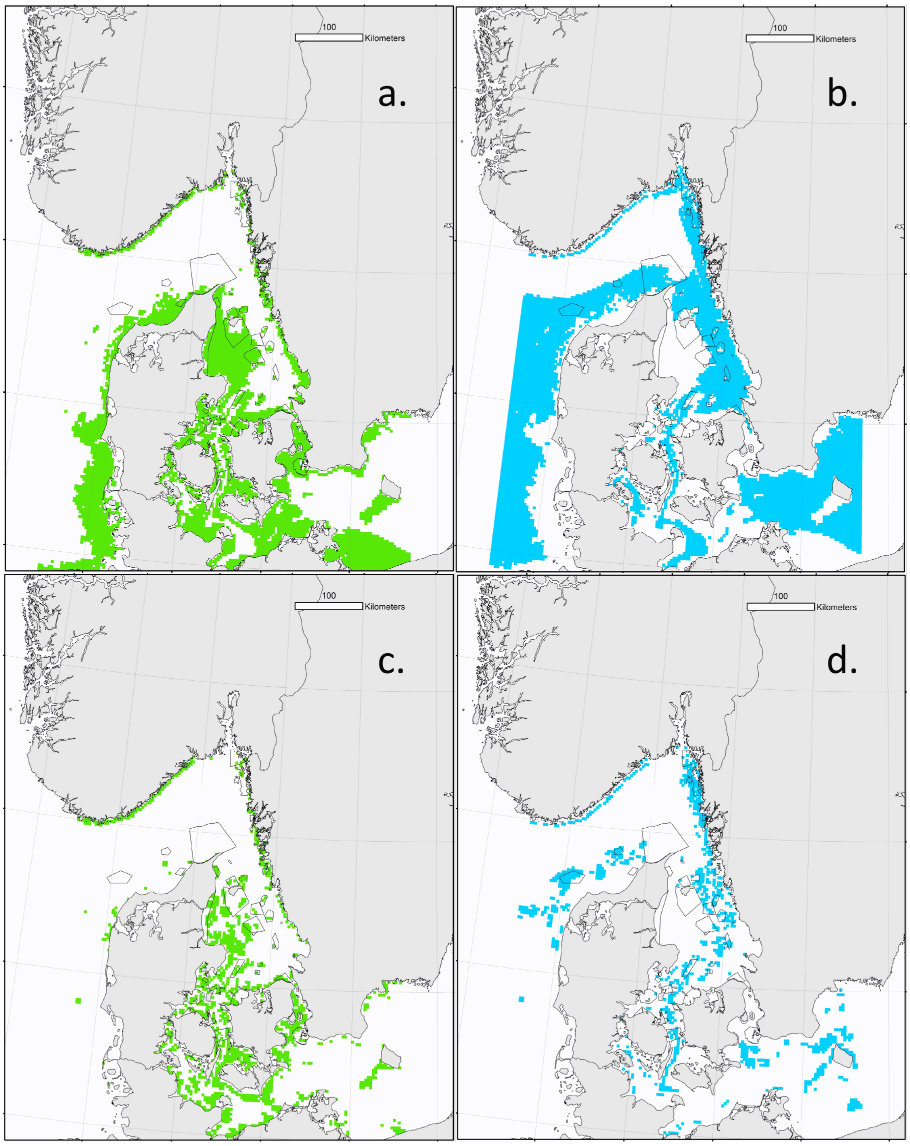


Figure 4. Maps showing model domain and the distribution of (a) shallow (1–20 m) and (b) deep (21–100 m) areas, and (c) shallow and (d) deep hard bottom habitats, based data of hard substrate developed within the EU-project BALANCE (Leth et al. 2008) and EUSeaMap (Cameron and Askew 2011). The marked areas are MPAs in the study region.

It is, however, important to point out that the BALANCE and EUSeaMap datasets of hard substrate in the study region has serious limitations as it also includes hard substrates covered with sediments, and it does not always include steep rocky coasts adjacent to soft sediment bottoms. In the study, we have supplement the BALANCE-data with rocky coastlines that we identified were missing. Taken together, the analyses of connectivity between hard bottom communities should be seen as an exercise and not as a representation of connectivity between existing hard bottom communities.

MPA-distribution

To be able to compare the effect of modeled metapopulation persistence in model-selected MPA-networks with existing networks of OSPAR-MPAs and other types of MPAs (e.g. Natura 2000 and marine reserves not designated as OSPAR-MPAs), the spatial distribution of MPAs was included in the model. Data on the location of MPAs within the study area (i.e. Kattegat and Skagerrak) were obtained in GIS-format from the County Administrative Board of Västra Götaland, Sweden, who also assisted in selecting MPAs that included protection of benthic habitats, and in identifying MPAs that included shallow and deep hard substrates. Since the BaltiX-model has a spatial resolution of 3.7 x 3.7 km^2 and a simplified coast line that poorly resolves small fjords and coastal archipelagoes, all MPAs smaller than 1 km^2 were excluded from the analyses, and larger MPAs located inside the coastal topography not resolved by the model were placed in the closest grid cell in the model. Because of this size-limitation, few Norwegain MPAs were included in the study. The large OSPAR-MPA *Bratten* (O-S-0520189) in the center of Skagerrak was not included in the analyses since it is located deeper than 100 m and is not included in the model domain where larvae were seeded. The large OSPAR-MPA *Skagen Gren* (O-S-0520189) north of Skagen in Jutland (Fig. 5) was included, although it is not clear how much protection it offers to the benthic habitat. In total, 31 OSPAR-MPAs were included in the study ranging in size from 1.4 to 2 711 km^2 (average size and diameter 270 km^2 and ca 18 km, respectively) covering a total area of 8 358 km^2, equivalent to approximately 15 % of the bottom area of Kattegat and Skagerrak (Fig. 5; see Table A1.4, Appendix A, for a complete list of included MPAs). In addition to the OSPAR MPA-network, we also assessed a second network where we included an additional 103, non-OSPAR MPAs found in the study area and in the Danish Straits. These MPAs ranged in size from 1.2 to 461 km^2 (average size and diameter 35 km^2 and ca 7 km, respectively) covering a total area of 3 620 km^2 (Fig. 5; Table A1.5, Appendix A). We assed the impact of these two MPA networks, i.e. only OSPAR-MPAs and all MPAs (a total of 134 MPAs covering 11 978 km^2) on metapopulation persistence with respect to connectivity for a range of organisms differing in larval traits.

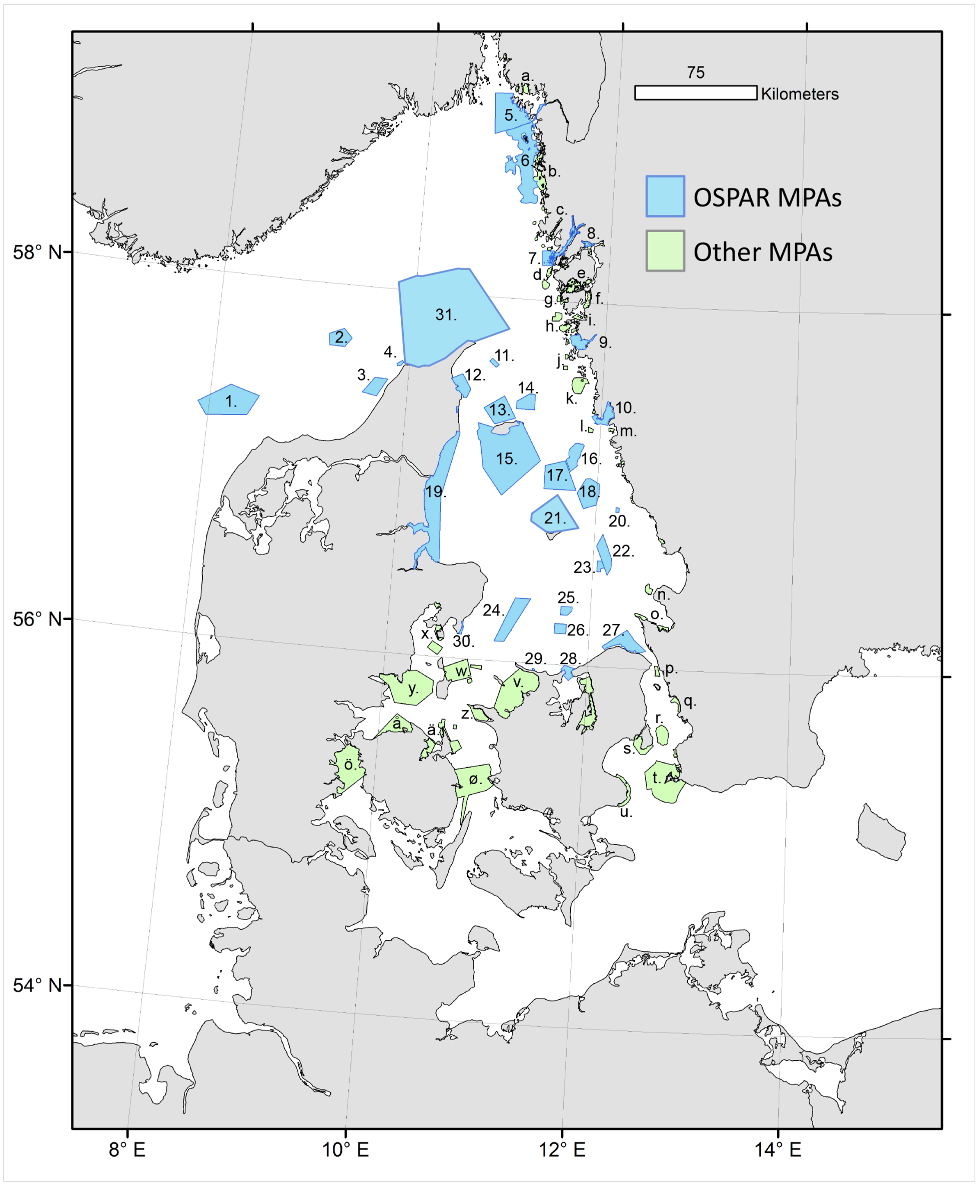


Figure 5. Map showing the model domain and the distribution of 31 OSPAR-MPAs (blue color; marked no. 1–31) found within the Kattegat-Skagerrak study area, and 103 other types of MPAs found in the study area and also in the Danish Straits (green color; the largest 29 marked a–ø) that were included in the model study. All included MPAs are found from 0–100 m depth.

OSPAR-MPAs: (1) Gule rev, (2) Store rev, (3) Lønstrup rødgrund, (4) Knudegrund, (5) Ytre Hvaler, (6) Kosterfjorden-Väderöfjorden, (7) Gullmarsfjorden, (8) Havstensfjorden, (9) Nordre älvs estuarium, (10) Kungsbackafjorden, (11) Herthas flak (12) Hirsholmene, (13) Nordre Rønner, (14) Læsø Trindel, (15) Havet syd Læsø, (16) Fladen, (17) Kims Top, (18) Lilla Middlegrund, (19) Ålborg bugd, (20) Morups bank, (21) Anholt, (22) Stora Middlegrund och Röde bank, (23) Store Middlegrund, (24) Schultz og Hastens grund, (25) Lysegrund, (26) Hesselø, (27) Gilleleje flak, (28) Hundested og Rørvig, (29) Ebbeløkke rev, (30) Kobberhage, (31) Skagen Gren.

Non-OSPAR MPAs: (a) Øra, (b) Tanumskusten, (c) Åbyfjorden, (d) Härmanö and Måseskär, (e) Stigfjorden, (f) Stenungssundskusten. (g) Härön and Toftenäs, (h) Pater Noster Skärgård och Klåverön, (i) Älgön-Brattön, (j) Ersdalen and Vinga, (k) Vrångöskärgården, (l) Nidingen, (m) Vendelseöarna, (n) Hallands Väderö, (o) Kullaberg-Skälderviken, (p) Knähaken, (q) Lundåkrabukten, (r) Saltholm, (s) Vestamager, (t) Falsterbohalvön, (u) Stevns rev, (v) Sejerø bugdt, (w) Stavns fjord, Munkegrunde and Hatterbarn, (x) Begtrup vig and Mejl Flak, (y) Horsens fjord, (z) Røsnæs, (å) Æbelö, (ä) Odense fjord, Fyns hoved and Romsö, (ö) Lillebælt, (ø) Centrale Storebælt. See Table A1.4 and A1.5 (Appendix A) for full names.

Larval types and habitats

The model experiment assessed 3 groups of larval types (1) *simple larval types*, (2) larvae of *shallow benthic organisms* and (3) larvae of *deep benthic organisms*. The simple larval types consisted of 4 combinations of distinct larval traits that were modeled mainly to explore how larval traits and ocean circulation interact and affect dispersal and connectivity in the area. The shallow and deep benthic larval types were designed to mimic dispersal of benthic organisms that inhabit depths of ≤20 m and 21–100 m, respectively, in the study area. The connectivity of the 3 groups were assessed both using all grid cells within the target depths, or only grid-cells with hard substrate within the target depths.

The *simple larvae* included 4 larval types that were dispersed for either 10 or 30 d, with a fixed drift depth of either 0–2 m, or below the pycnocline at 24–26 m. All larval types were released from April to August (Table A1.6, Appendix A). For of each larval type, 49 trajectories were released from all grid cells in the study domain between 1–100 m depth (a total of 8 992 grid cells), between April and August, during 8 years (1995–2008).

The second and third group (*shallow* and *deep benthic organisms,* respectively) consisted of 5 larval types each carefully chosen to represent selected groups of benthic plants and animals found above or below 20 m depth on rocky reefs and soft sediment habitats. The assessed drift depths and pelagic larval duration (PLD) varied between 0 to 50 m, and 5 to 60 d, respectively, whereas most larvae were released from April to August each year (Table A1.6, Appendix A). The chosen drift depths, PLDs and larval release dates were based on the results from the plankton survey and literature search, and when designing the larval types the goal was to include the dominant taxa from shallow and deep benthic habitats in the study area, as well as including as many as possible of the organisms from OSPAR's list of threatened and/or declining species (Table A1.3, Appendix A). Since many larval taxa had similar traits, the 10 larval types assessed in the model included dominant organisms from both hard and soft sediment habitats (Table A1.1 and A1.2, Appendix A). The empirical data demonstrated that the same larval taxa often had a wide depth distribution at any point in time why the different larval types were given a distribution of different drifts depths and PLDs that reflected the empirical data (Table A1.6, Appendix A). Only fixed drift depths were assessed since the result from the plankton survey indicated ontogenetic or diel changes in larval depth for only a minority of the species. For those taxa the results may be less accurate. For each larval type, 49 trajectories were released on the 15th of each month during the stated larval release periods, during 8 years. Shallow benthic trajectories were only released from and allowed to settle on grid cells with a depth between 1–20 m, and deep benthic trajectories only on grid cells with a depth between 21–100. In total 335 million trajectories were modeled in the study.

The reason for separating the habitats into above and below 20 m is that pulses of low salinity water can affect bottoms down to approximately 20 m in Kattegat and Skagerrak, which negatively affects groups of organism intolerant to low salinity (e.g. echinoderms, certain crustaceans, polychaetes, etc.). For this reason, the composition and diversity of the benthic communities is quite different below and above 20 m in this area, which is reflected in different criteria for determining the ecological status of the benthic communities above and below 20 m in these waters (according to the EU Water Framework Directive; Naturvårdsverket 2007). Moreover, the maximum depth for macroalgae is around 20 m along the Swedish west coast (Naturvårdsverket 2007), why 20 m also approximately separates the photic and the aphotic zone in this area.

3.2.1.4 Dispersal and connectivity analyses

At the end of the pelagic larval period, the dispersal distance of each trajectory was estimated from the release position. Net distances were calculated from the great-circle distance (Sinnott 1984). Dispersal distances waere analyzed for all 14 larval types separately.

In the analyses of connectivity, only trajectories that were located above the same depth and substrate type as from where it was released was considered to have settled successfully and was included to estimate the connectivity between any two grid cells. If a trajectory ended up above a different depth or substrate class it was scored as lost, and it was not included in the connectivity matrices. We constructed connectivity matrices for all 14 larval types separately for all 4 habitat-combinations (shallow and deep, all areas and only hard substrate).

3.2.1.5 Finding the optimal network

EPT-method

To identify the optimum network of MPAs with respect to the larval connectivity between sites we applied the new method using *eigenvalue perturbation theory* (EPT; Nilsson Jacobi and Jonsson 2011). An optimum network is here defined as the network of a given size that maximizes the growth rate of the whole metapopulation when its abundance is low (far from carrying capacity) which is the typical case for threatened populations. A simplistic explanation of the EPT method is that the method estimates how good each grid cell is at both receiving settling larvae (source-strength) and at supplying settling larvae to other grid cells (sink-strength) and ranks all grid-cells after their combined source-sink-strength. The highest ranked grid cells thus represent the most valuable areas and local populations in the metapopulation for that particular larval type. We carried out EPT-analyses on the matrices from all different larval types and habitat-combinations.

Each larval type will generate a unique optimum network and when the objective is to protect multiple species representing several larval types the challenge is to find a consensus network that will offer sufficient protection for all target species. We have here developed novel theory that can find such consensus networks based on multiple EPT ranking lists each representing a single larval type (Jonsson et al. *in prep*). This identification of multiple-species networks requires that some boundary conditions are provided, which in short is some statement of the minimum growth rate required for the least protected species.

Metapopulation model

To evaluate if the grid cells identified by the EPT-method really represented the best MPA network we carried out metapopulation modeling where we explored the effect of protection implementing different networks including the present real-world MPA networks, the EPT-based optimum networks, and randomly selected networks. The simplistic model considered all grid cells within the study domain (all 4 habitat combinations) as local populations of an annual organism connected by dispersal through the connectivity matrix. Every grid cell was given the same growth rate except those grid cells included in MPA networks which was assumed to grow 20 % faster because of being protected. Growth of local populations was density-dependent and carrying capacity was reached assuming a hockey-stick function (Barrowman and Myers 2000). To simulate stochastic reductions in population abundance, e.g. caused by hydrologic and climatic factors, the metapopulation was stochastically reduced by 95 % with an expected interval of 8 years. Each model simulation was run for 100 years and this was repeated 100 times. For each model simulation the mean size of the metapopulation at low abundance (below 5 % of carrying capacity) was recorded without and with protection (as a result of an MPA network). The rationale for only recording the metapopulation size at low abundances is that this is when protection is assumed to be most important. Mathematically the population model can be formulated as:

$$P_{t+1} = \chi(t)\cdot \min\left(R\cdot C\cdot P_t,\ 1\right)$$
$$\chi(t) = \left\{ \begin{array}{l} \varepsilon = 0.05 \text{ with probability } 0.2 \text{ at each time step} \\ \varepsilon = 1 \text{ otherwise} \end{array} \right\}$$

where P_t is the vector of all local population sizes at time t, R is a diagonal matrix with the reproduction rates for each local population, C is the connectivity matrix specifying the dispersal of larvae between all local populations, and $c(t)$ is a stochastic variable specifying reductions of the metapopulation. Note that the reproductive matrix R contains the effect of the MPA protection through the 20 % higher rates at the local populations included in the MPA network.

To compare the effect of the present MPA-network and optimum networks consisting of the grid cells selected by the EPT-method, the total size of the metapopulations (i.e. metacommunities) was compared between a network consisting of only OSPAR MPAs, a network consisting of all MPAs (23–81 % larger depending on habitat), optimum EPT-networks of the same sizes, and a randomly selected network of the same sizes (as a control). This comparison was done for all 4 habitats combinations. In addition, the effect on only the populations inside the networks, and the effect in the eastern Skagerrak area (the Bohus coast) were assessed. The Bohus area on the Swedish northeast coast was of particular interest due to the strong effect of the assymetric circulation on dispersal detected by the biophysical model.

3.3 RESULTS

3.3.1 Simple larval types

3.3.1.1 Dispersal distance

The dispersal distance of trajectories with 4 simple larval traits were strongly affected by the drift depth and the pelagic larval period (PLD), as well as by the area from where they had been released in the model (Fig. 6). Trajectories drifting at the surface were transported large distances, 40–90 km after 10 d, and 80–140 km after 30 d in most areas. However there were large regional differences in the transport distances. Surface drifting trajectories released in the central part of southern Kattegat, the Öresund strait, and close to coast in western Kattegat and Swedish Skagerrak were transported about half the distance (approximately 40 and 80 km after 10 and 30 d respectively) compared to trajectories released in the Danish straits, and remaining areas of Kattegat and Skagerrak (approximately 80 and 130 km after 10 and 30 d respectively; Fig. 6).

In contrast, trajectories drifting below the pycnocline at 24–26 m depth were transported short distances, 5–50 km after 10 d, and 10–80 km after 30 d in most areas. Again, there were large regional differences in the transport. Trajectories drifting at 24–26 m were transported very short distances in western Kattegat and close to the coast in eastern Kattegat (approximately 5–20 km after 30 d), but large distances in deeper offshore areas in Skagerrak (approximately 100–140 km after 30 d; Fig. 6). These strong regional differences, and large effects of larval traits on larval dispersal distances suggest that the potential for self-recruitment within MPAs will be strongly dependent on the local oceanographic conditions and the larval traits of the targeted species.

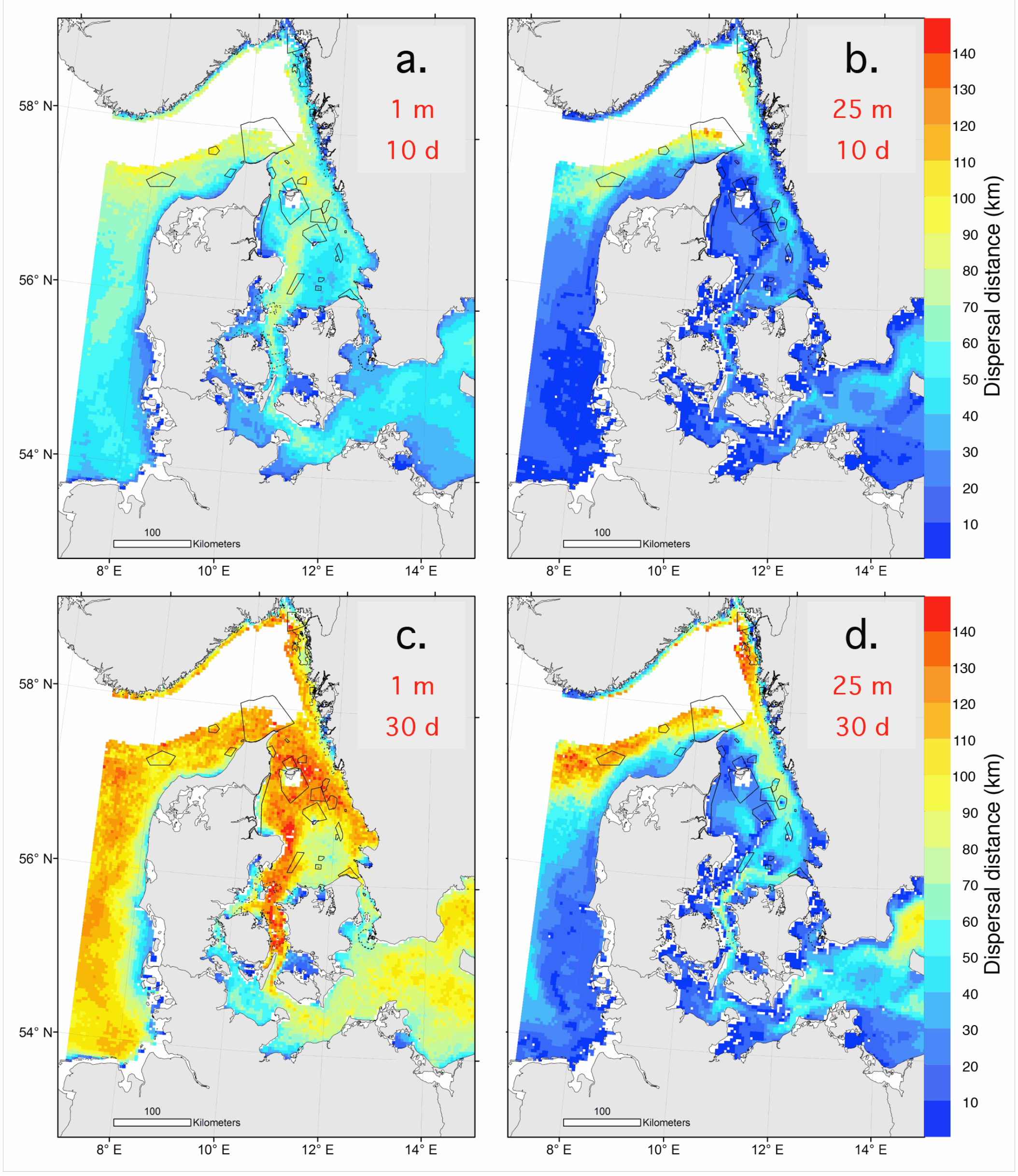


Figure 6. Model results - dispersal distance for simple larvae. Maps showing the average dispersal distance (km) for each grid cell where the trajectories were released for 4 different simple larval types, (a) 0–2 m drift depth and 10 d PLD, (b) 24–26 m drift depth and 10 d PLD (c) 0–2 m drift depth and 30 d PLD and (d) 24–26 m drift depth and 30 d PLD. MPAs are marked on the maps with black lines.

3.3.1.2 Source-sink analyses in 5 regions

All depths and habitats

To assess connectivity between the 5 regions of the study area (see Fig. 3), the most important grid cells in supplying trajectories to a region (source-areas), and the grid cells that received the most trajectories from a region (sink-areas) were identified for each region. This source-sink analysis demonstrated a strong effect of larval traits where trajectories drifting below the pycnocline for 10 d mainly stayed within the region where they were released, whereas trajectories that were dispersed in surface water for 30 d were mainly dispersed outside of the region of release, consistent with the analyses of dispersal distances. Some surface drifting trajectories were transported surprisingly large distances in 30 d; e.g. the region *eastern Skagerrak* (NW coast of Sweden) had source areas from the southwestern part of the Baltic Sea as well as from the North Sea area (Fig. 7a), dispersal distances of at least 470 km.

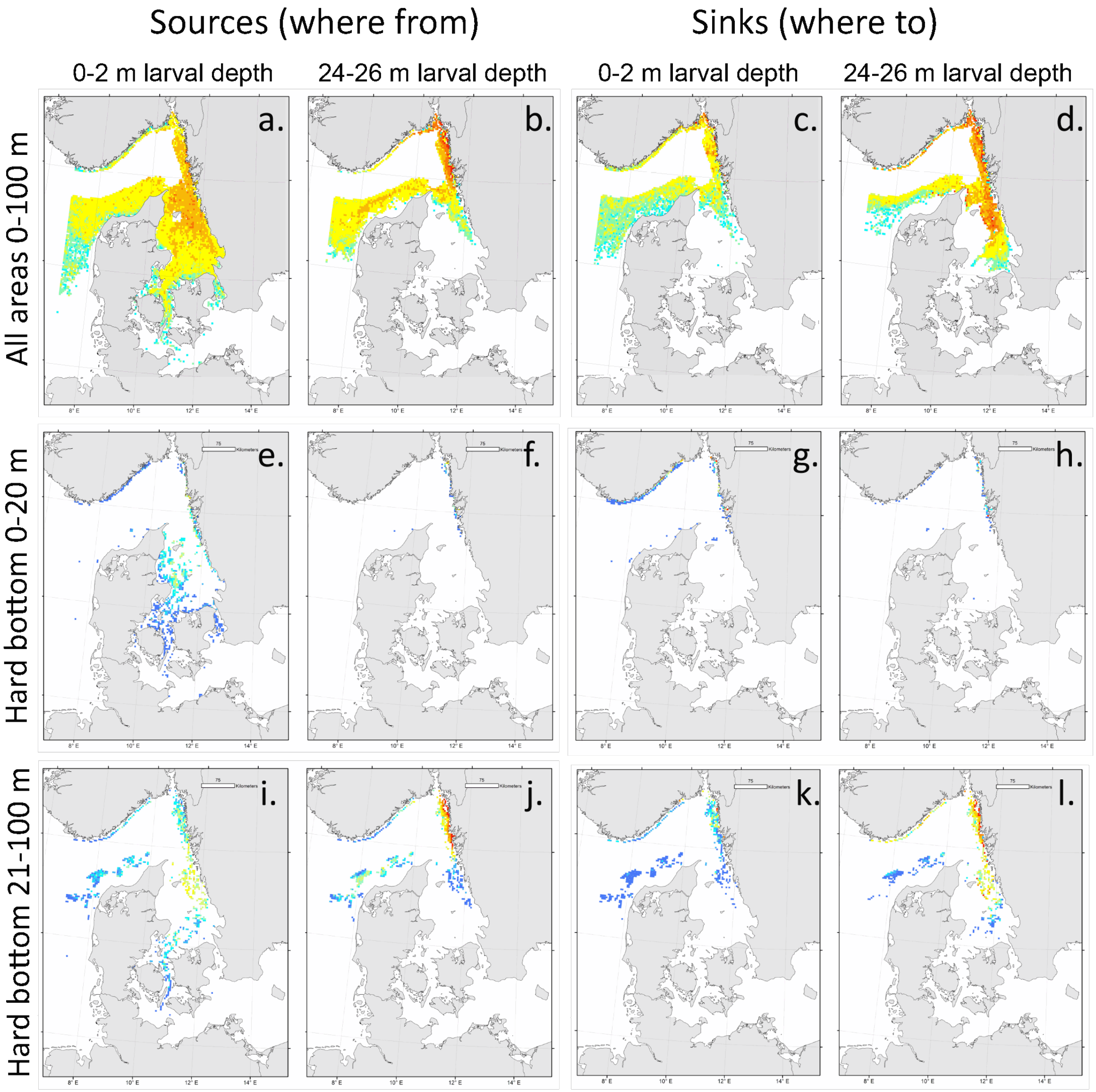


Fig. 7. Model results - source-sink analyses for simple larval types 3 and 4. Analyses for eastern Skagerrak (NW coast of Sweden) of modeled larvae swimming at the surface (0–2 m) and below the pycnocline at 24–26 m during a 30 d larval phase. Source-areas that have provided eastern Skagerrak with larvae (a–b, e–f, i–j), and sink-areas where larvae released in eastern Skagerrak have settled (c–d, g–h, k–l) for larvae that have been released and settled on all bottom areas at 1–100 m depth (a–d), released and settled only on shallow (0–20 m) hard bottoms (e–h), and on deep (21–100 m) hard bottoms (i–l). Red to blue color denotes high to low frequency of trajectories. White color denotes zero trajectories.

Importantly, the analysis also revealed an asymmetric circulation in the study area where surface water was transported mainly northward in Kattegat and along the west coast of Sweden, and west out of the model domain along the south coast of Norway, whereas water below the pycnocline was transported southward along the west coast of Sweden. This transport is consisted with a baroclinic flow of surface water from the Baltic Sea water out of Kattegat and Skagerrak, and a residual flow of deep water southward into Kattegat (Andersson and Rydberg 1993, Fonselius 1995). For the NW coast of Sweden this estuarine circulation had important consequences for the connectivity. Most surface drifting larvae with a PLD of 30 d were transported out of the model domain (as seen as a low frequency of trajectories that ended up within the study area; Fig. 7c), whereas trajectories drifting below the pycnocline to a large extent were transported southward into Kattegat, resulting in substantially higher number of trajectories that remained within the study area (Fig. 7d). In contrast to the depth-dependent asymmetric connectivity between Kattegat and Skagerrak, transportation from the North Sea and western Skagerrak region to the NW coast of Sweden was relatively high both for surface- and deep-drifting trajectories (Fig. 7ab), indication that the North Sea is an important source area for the Swedish west coast.

Shallow hard bottom habitats

The simulations where trajectories were only released from, and allowed to "settle" in shallow (≤20 m depth) hard substrate habitats resulted in overall much lower and different connectivity due to the lack of the habitats. Comparing the results for the NW coast of Sweden, the source area for surface drifting trajectories were mainly the shallow areas of western Kattegat and the Danish straits (Fig. 7e), and the sink areas were mainly within the Swedish NW coast and along the south coast of Norway (Fig. 7g). For trajectories dispersing below the pycnocline, the lack of shallow hard bottom habitats in western Skagerrak resulted in much lower connectivity that when no habitat restriction were used, and the source and sink area for the NW coast of Sweden was mainly within the region (Fig. 7fh).

Deep hard bottoms

Assessing connectivity only between deep (20-100 m) hard substrate habitats resulted in much higher connectivity compared to shallow hard habitats, although the total area of the two habitats was similar (Fig. 4cd). Comparing the results for the NW coast of Sweden, the main source areas for surface drifting trajectories were both the Danish straits, Eastern Kattegat, western Skagerrak and within the Swedish NW coast (Fig. 7i), and the sink areas were mainly within the Swedish NW as well as western Skagerrak and the south coast of Norway (Fig. 7k). For trajectories dispersing below the pycnocline, the connectivity was substancially higher compared to shallow hard habitats, with the main source areas within the Swedish NW coast as well as western Skagerrak, and the main sink areas within the Swedish NW coast as well as eastern Kattegat. The higher connectivity for deep compared to shallow hard habitats appeared to be a result of deep hard habitats along the connectivity paths in eastern Kattegat and in Western Skagerrak (Fig. 7).

3.3.1.3 Optimal MPA-networks

Using the connectivity matrices and the method using *eigenvalue perturbation theory* (EPT) to identify the optimum network of MPAs with respect to the larval connectivity showed a concentration of selected MPA-sites within the straits between the Baltic Sea and Kattegat, in western Kattegat, and along the west coast of Jylland, but few selected areas along the west coast of Sweden and south coast of Norway (Fig. 8). The lack of selected sites in the latter areas was likely a result of the asymmetric circulation caused by the Baltic current, transporting larvae above the pycnocline along these coast northward and out of the study region, making these areas poor source-populations for the network.

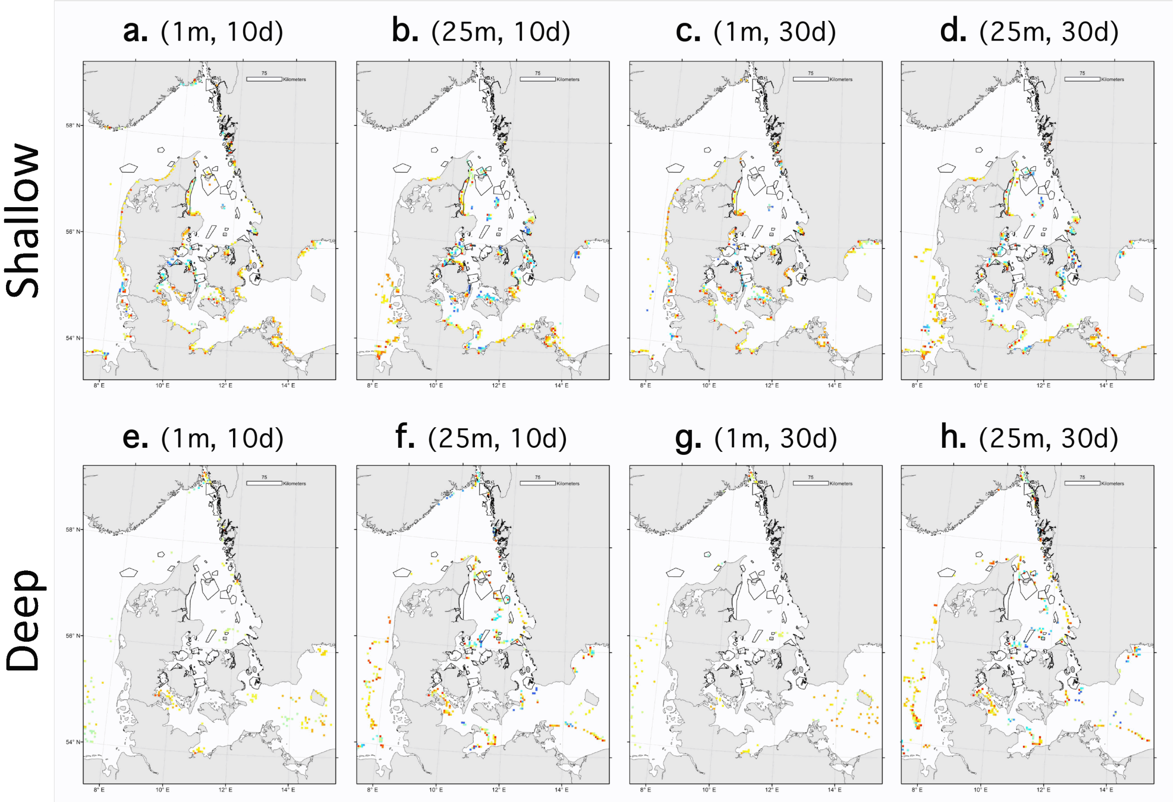


Fig. 8. Model results - optimal networks for simple larval types on shallow and deep bottoms. Results from the analyses using eigenvalue perturbation theory (EPT) to identify the best grid cells for an optimal network for larval connectivitiy, for 4 different larval types in shallow (1-20 m; a-d) and deep (21-100 m; e-h) areas (i.e. all types of habitats) of the model domain. Red to blue color denotes high to low rank of areas.

These analyses also identified important differences in the optimal network for different larval types within the Kattegat-Skagerrak area. For larval trajectories that were only released and allowed to settle in shallow areas (1–20 m), surface drifting larval types had a network with a number of important sites along the central part of the Swedish west coast and the Norwegian coast, particularly larvae with short PLD, whereas very few sites were found in southeastern part of Kattegat in the Öresund strait. In contrast, deep drifting larval types had a high number of high ranked sited in the Öresund strait, but almost non in Skagerrak (Fig. 8a–d).

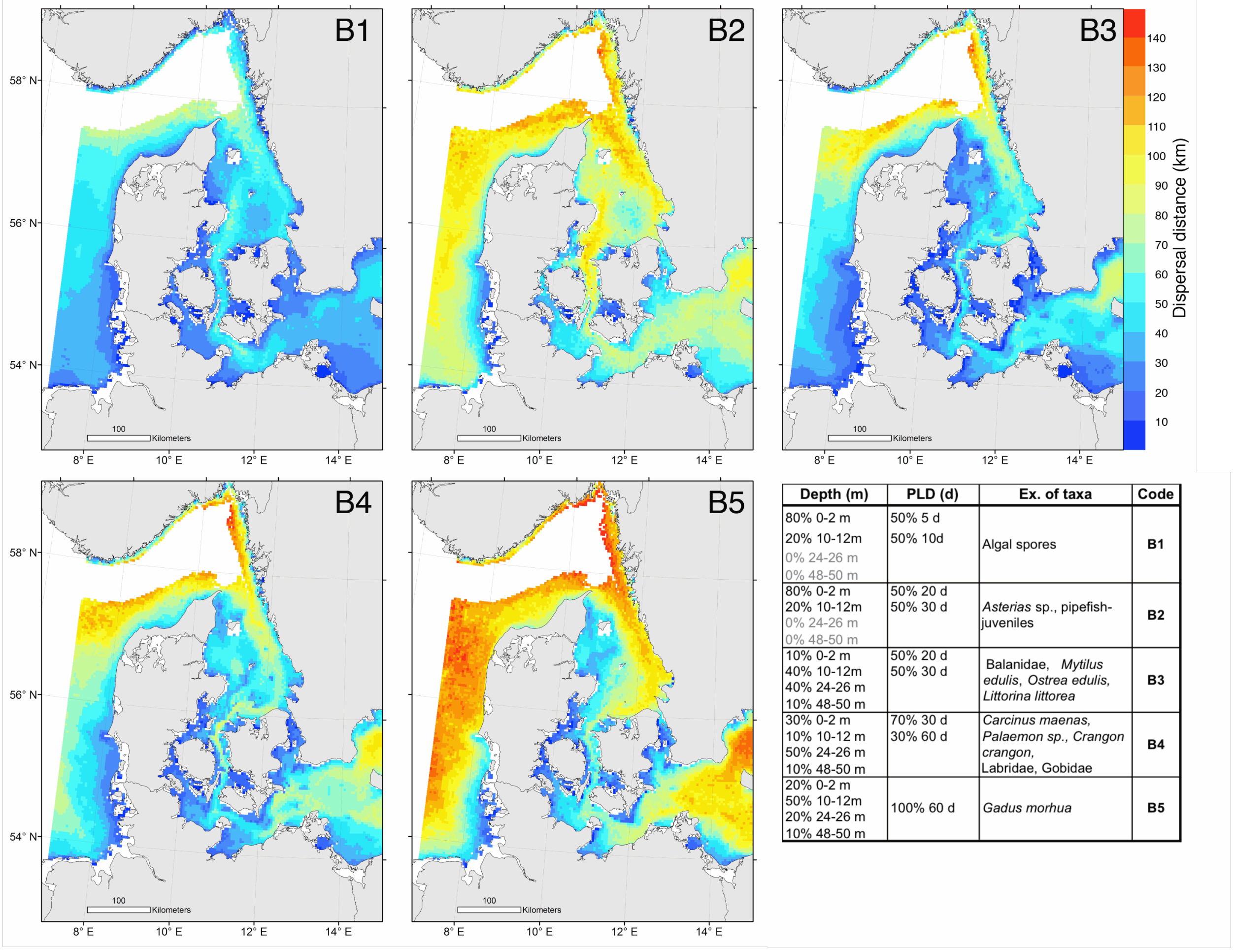
For trajectories that were released and settled only in deep areas (21–100 m), surface-drifting larvae had very few selected sites within the Kattegat-Skagerrak area, whereas deep drifting larvae had a high number of important sites within the Kattegat area (Fig. 8e–h). The higher number of sites for deep drifting larvae was likely a result of the residual southward transport of deep water of the estuarine circulation in the study area, keeping deep-drifting larvae within the Kattegat area and increasing connectivity.

If these results are a representation of the true connectivity in the study area (se limitation of the study below) they have important implications for the design of functional MPA-network in the study area since the circulation along the Swedish and Norwegian Skagerrak coast makes these areas dependent on larvae from sources in southern Kattegat and the North Sea.

3.3.2 Shallow and deep hard bottom ecosystem

3.3.2.1 Dispersal distance per larval type shallow and deep bottoms

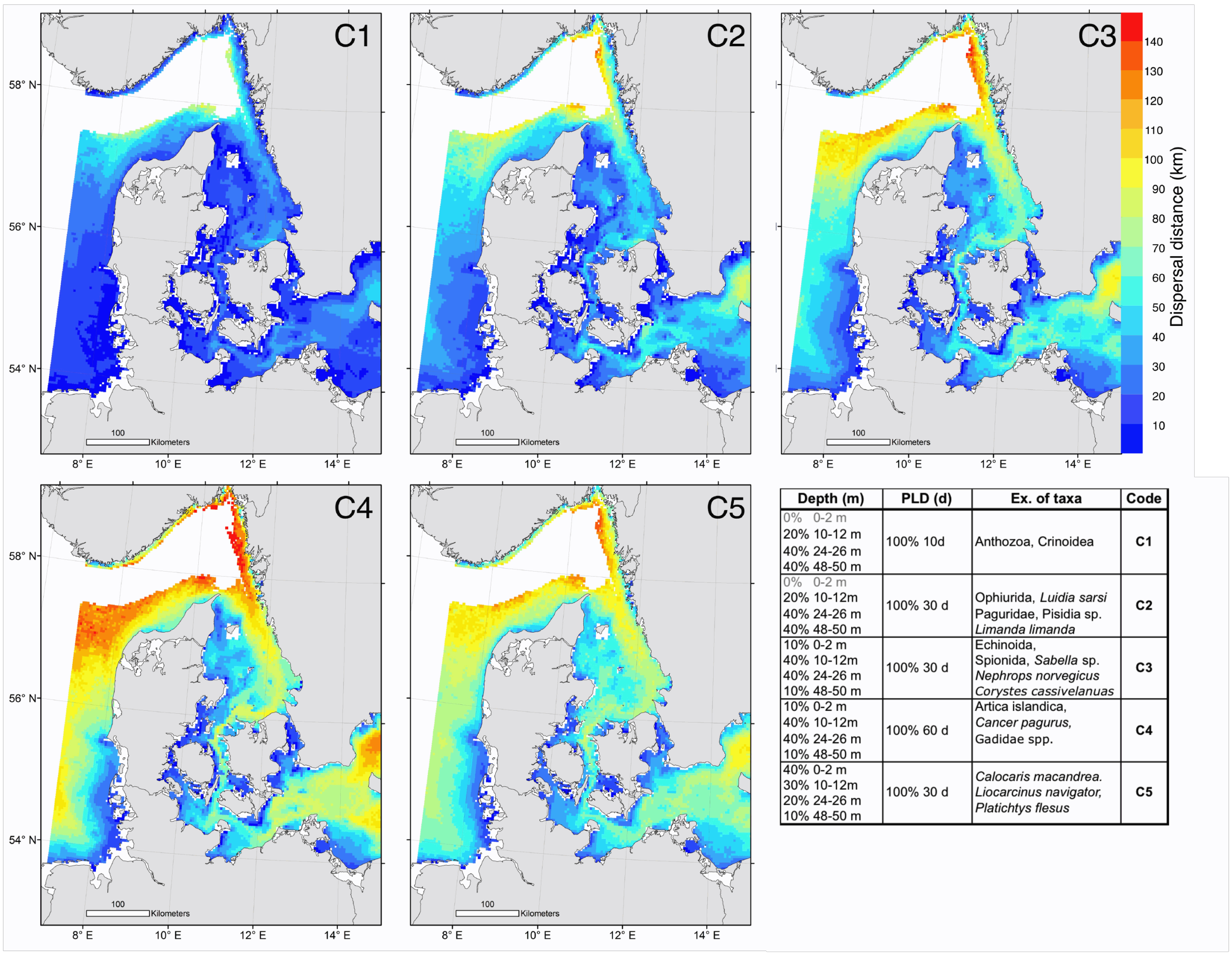
The dispersal distance of trajectories with larval traits chosen to represent selected benthic plants and animals found at shallow (0–20 m) depth on rocky reefs and soft sediment habitats were strongly affected by the drift depth and the pelagic larval period, as well as by the area from where they had been released in the model (Fig. 9), similar to the simple larval types. Organisms with a majority of larvae drifting in surface waters (e.g. asteroid sea stars; B2) were dispersed 2–4x further distances than organism with a majority of the larvae drifting below the pycnocline (e.g. bivalves and gastropods; B3). Cod larvae, with a PLD of 60 d and a majority of larvae above the pycnocline were dispersed the largest distances; >100 km in most areas (Fig. 9, B5).



Depth (m)	PLD (d)	Ex. of taxa	Code
80% 0-2 m 20% 10-12m 0% 24-26 m 0% 48-50 m	50% 5 d 50% 10d	Algal spores	**B1**
80% 0-2 m 20% 10-12m 0% 24-26 m 0% 48-50 m	50% 20 d 50% 30 d	*Asterias* sp., pipefish-juveniles	**B2**
10% 0-2 m 40% 10-12m 40% 24-26 m 10% 48-50 m	50% 20 d 50% 30 d	Balanidae, *Mytilus edulis*, *Ostrea edulis*, *Littorina littorea*	**B3**
30% 0-2 m 10% 10-12 m 50% 24-26 m 10% 48-50 m	70% 30 d 30% 60 d	*Carcinus maenas*, *Palaemon sp.*, *Crangon crangon*, Labridae, Gobidae	**B4**
20% 0-2 m 50% 10-12m 20% 24-26 m 10% 48-50 m	100% 60 d	*Gadus morhua*	**B5**

Figure 9. Model results - dispersal distance for shallow bottom larval types. Maps showing the average dispersal distance (km) for each grid cell where the trajectories were released for 5 different larval types (B1–5) representing organisms living on depth <20 m in the Kattegat and Skagerrak area.

The dispersal distance of trajectories chosen to represent benthic animals living below 20 m depth and with larvae that to a larger extent were drifting below the pycnocline were also affected by larval traits and the release area, but in general dispersed shorter distances compared to the shallow bottom organisms (Fig. 10). Organisms that exclusively drifted at or below the pycnocline and with short PLD (e.g. anthozoans and cnidarians; C1) were dispersed <40 km in most areas, whereas larvae of most decapods and fish taxa with longer PLDs and larvae drifting also in surface waters (C2–5) were dispersed >100 km in the coastal regions of Skagerrak (Fig. 10).



Depth (m)	PLD (d)	Ex. of taxa	Code
0% 0-2 m 20% 10-12 m 40% 24-26 m 40% 48-50 m	100% 10d	Anthozoa, Crinoidea	**C1**
0% 0-2 m 20% 10-12m 40% 24-26 m 40% 48-50 m	100% 30 d	Ophiurida, *Luidia sarsi* Paguridae, Pisidia sp. *Limanda limanda*	**C2**
10% 0-2 m 40% 10-12m 40% 24-26 m 10% 48-50 m	100% 30 d	Echinoida, Spionida, *Sabella* sp. *Nephrops norvegicus* *Corystes cassivelanuas*	**C3**
10% 0-2 m 40% 10-12m 40% 24-26 m 10% 48-50 m	100% 60 d	Artica islandica, *Cancer pagurus,* Gadidae spp.	**C4**
40% 0-2 m 30% 10-12m 20% 24-26 m 10% 48-50 m	100% 30 d	*Calocaris macandrea.* *Liocarcinus navigator,* *Platichtys flesus*	**C5**

Figure 10. Model results - dispersal distance for deep bottom larval types. Maps showing the average dispersal distance (km) for each grid cell where the trajectories were released for 5 different larval types (C1–5) representing organisms living on depth 20–100 m in the Kattegat and Skagerrak area.

3.3.2.2 Multispecies source-sink analyses for shallow and deep hard bottoms

To assess connectivity between the 5 regions of the study area for benthic communities found on shallow hard bottom habitats (0–20 m), the most important source- and sink-areas for all shallow larval types combined (B1–5) were identified for each region (Fig. 11 a–j). Likewise, the most important source- and sink-areas for all deep larval types (C1–5) released and settling on deep hard bottom habitats (21–100 m) were identified for each region (Fig. 11 k–t).

These multispecies analyses that combined the different connectivities of the 5 larval types showed source-sink pattern that reflected both differences in dominating larval traits and the availability of shallow and deep hard bottom habitats in the different regions. For shallow hard bottom communities, western Kattegat and the Danish straits constituted the major source-areas for all regions except western Skagerrak (N of Jutland), which has few shallow hard bottom areas and is relatively poorly connected with other regions (Fig. 11 a–e). Western Kattegat also had high connectivity within the region, which was also found to a lesser extent in northern Skagerrak along the south coast of Norway. The Swedish NW coast received larvae mainly from Kattegat, but exported larvae mainly to Norway (Fig. 11c,h), indicating a unidirectional transport of larvae.

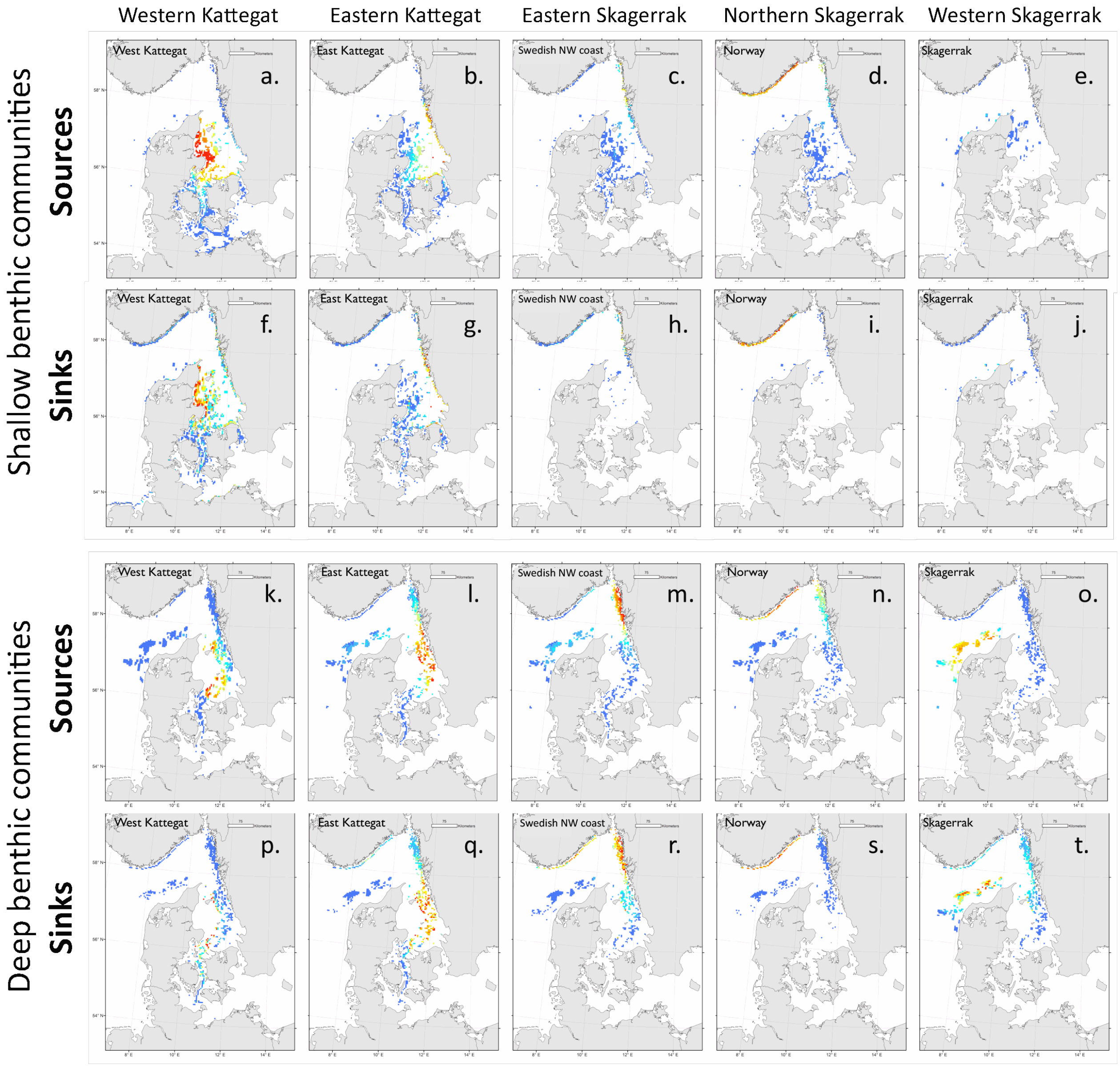


Fig. 11. Multispecies source-sink analyses for shallow and deep hard bottom habitats. Results of the source-sink analyses for shallow hard bottom habitats (larval types B1–5; a–j) and deep hard bottom habitats (larval types B1–5; a–j) for the 5 regions of the study area (see text for explanations). Red to blue color denotes high to low frequency of trajectories. White color denotes zero trajectories.

For deep hard bottom communities, a different connectivity pattern was seen with higher connectivity within regions, and where eastern Kattegat and western and eastern Skagerrak constituting important source areas (Fig. 11 k–t). Due to the few deep hard bottom areas in western Kattegat, this region was less important for the connectivity to other areas. In contrast to shallow bottoms, the deep hard bottoms along the NW coast of Sweden showed a high degree of connectivity both within and between regions (Fig. 11 m,r). The higher degree of connectivity for deep hard bottom communities along the Swedish NW coast were likely due to a higher proportion of deep drifting larvae among the deep larval types, and more area of deep compared to shallow hard bottom habitats in eastern Skagerrak (Fig. 4).

3.3.2.3 Optimal MPA-networks

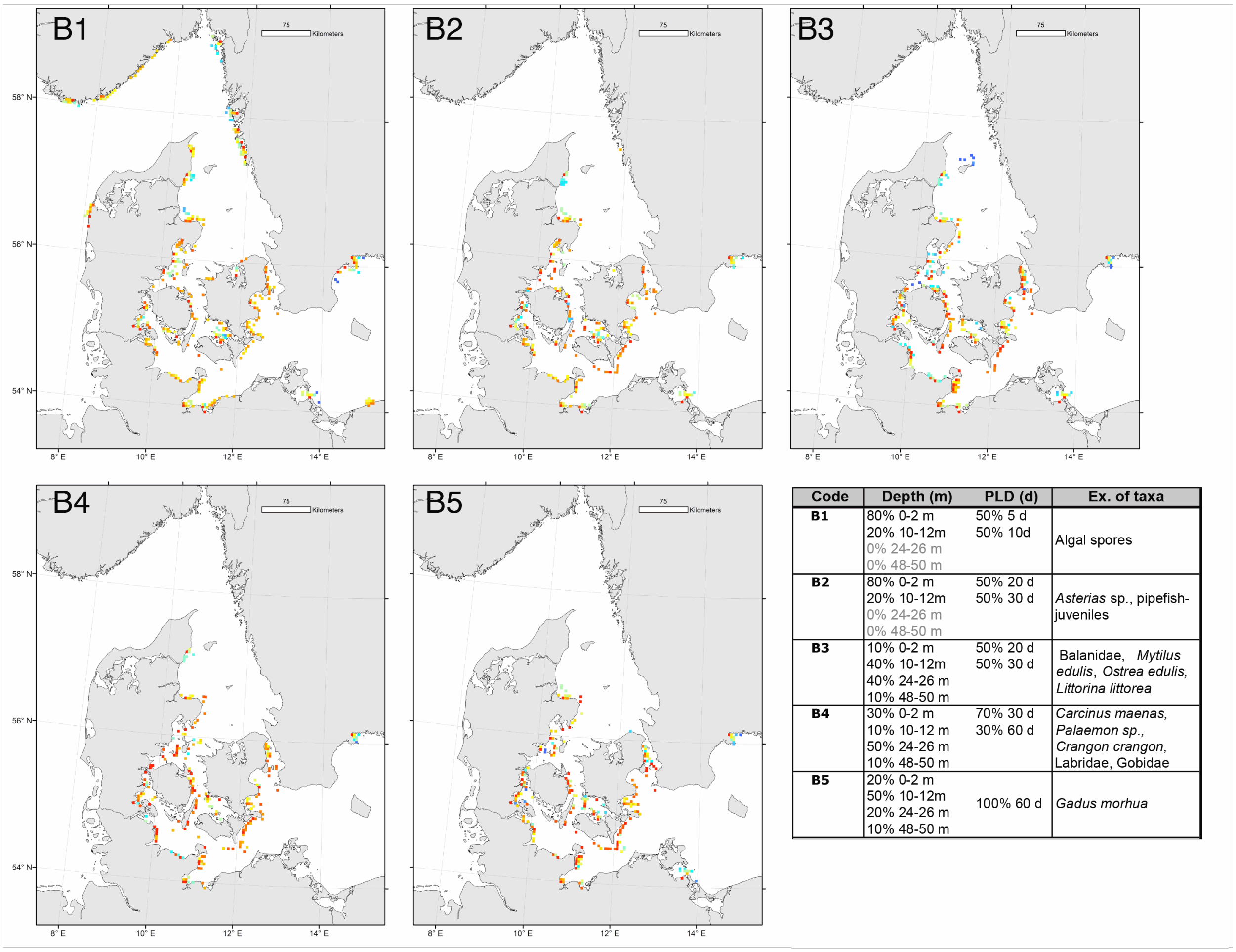
Shallow larval types on hard bottoms

Using the connectivity matrices and the EPT-method to identify the optimum network of MPAs (with respect to the larval connectivity) for larval types living on shallow hard bottoms showed a concentration of selected MPA-sites within the Danish Straits and in western Kattegat, but no selected areas in Skagerrak for a all but one larval type (Fig. 12). Only the larval type with a very short PLD (5–10 d) and propagules drifting in the surface (B1; e.g. algal spores) had an optimum network with MPAs selected also along the west coast of Sweden, southern Norway and the NW coast of Jutland (Fig. 12, B1). The lack of selected MPA-sites along the west coast of Sweden and southern Norway was likely a result of the asymmetric circulation caused by the Baltic current, which transported larvae above the pycnocline along these coast northward and out of the study region, making these areas poor source-populations for the network. In addition, Skagerrak had fewer shallow hard bottom areas than western Kattegat (according to the habitat data used in the study), decreasing connectivity further in the former area where only organisms with short PLDs and dispersal distances could function well in a network.

Deep larval types on hard bottoms

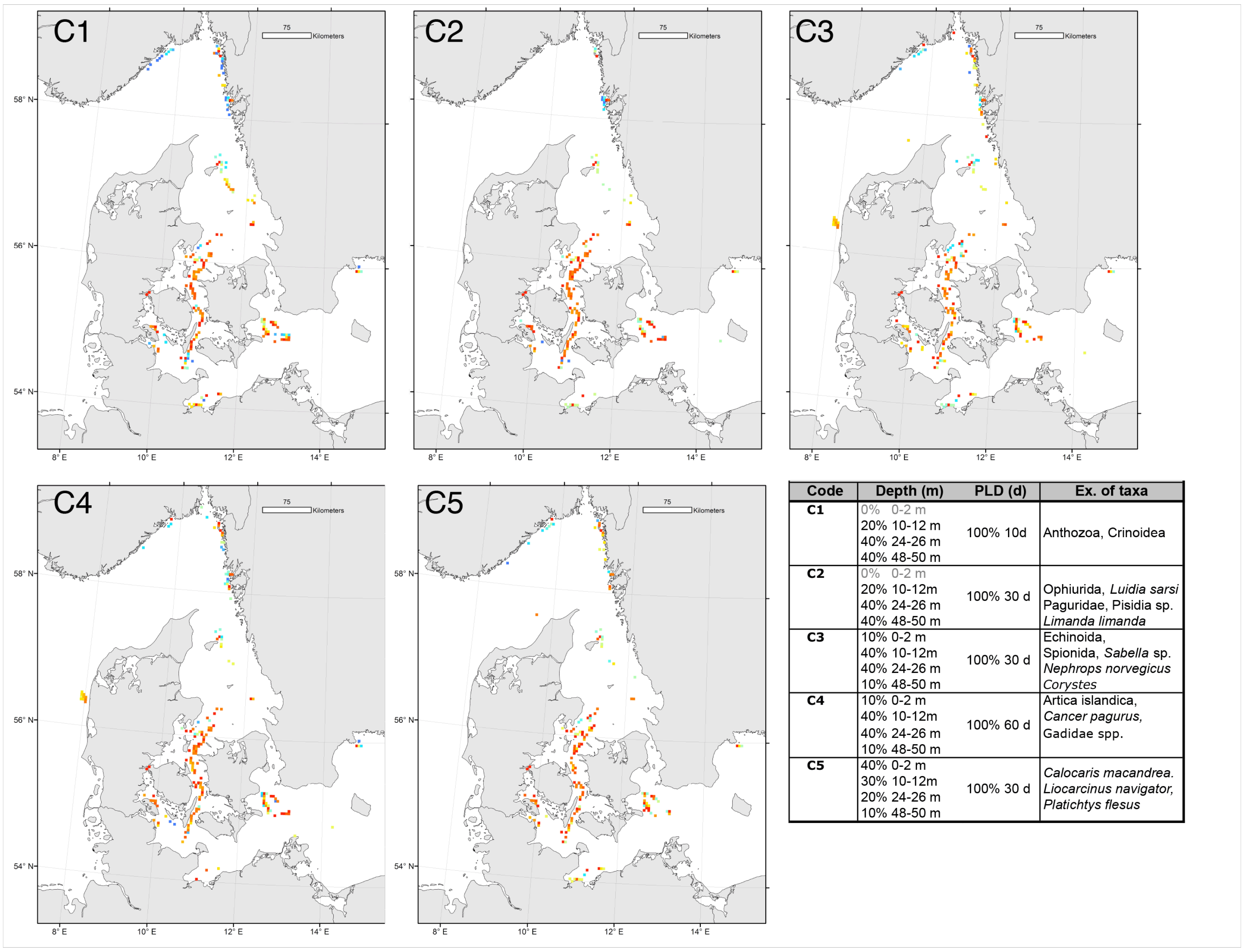
In contrast to shallow hard bottom communities, larval types living on deep hard bottoms showed a concentration of selected MPA-sites also along the Swedish NW coast and the south coast of Norway for most larval types (Fig. 13). As indicated in the source-sink analysis, this difference was likely due to a higher proportion of deep drifting larvae among the deep larval types, and a larger extent of deep compared to shallow hard bottom habitats in Skagerrak.

One important difference between the results from the source-sink analysis and the EPT-analysis is that the western Skagerrak area (north of Jutland) constituted an important source area for several regions in Kattegat and Skagerrak (Fig. 11), but few MPA-sites were still selected in this region by the EPT-method (Fig. 13). The difference indicate that western Skagerrak, although an important source area was less important as a sink area (received few larvae from other areas), likely a result of the unidirectional Jutland current, making the region function less well in a MPA-network.



Code	Depth (m)	PLD (d)	Ex. of taxa
B1	80% 0-2 m 20% 10-12m 0% 24-26 m 0% 48-50 m	50% 5 d 50% 10d	Algal spores
B2	80% 0-2 m 20% 10-12m 0% 24-26 m 0% 48-50 m	50% 20 d 50% 30 d	*Asterias* sp., pipefish-juveniles
B3	10% 0-2 m 40% 10-12m 40% 24-26 m 10% 48-50 m	50% 20 d 50% 30 d	Balanidae, *Mytilus edulis*, *Ostrea edulis*, *Littorina littorea*
B4	30% 0-2 m 10% 10-12 m 50% 24-26 m 10% 48-50 m	70% 30 d 30% 60 d	*Carcinus maenas*, *Palaemon sp.*, *Crangon crangon*, Labridae, Gobidae
B5	20% 0-2 m 50% 10-12m 20% 24-26 m 10% 48-50 m	100% 60 d	*Gadus morhua*

Fig. 12. Model results - optimal networks for shallow bottom larval types. Results from the analyses using eigenvalue perturbation theory (EPT) to identify the best grid cells for optimum networks in regards of larval connectivity for the 5 shallow bottom larval types assessed for shallow hard bottom habitats in the study domain. Red to blue color denotes high to low rank of areas.



Code	Depth (m)	PLD (d)	Ex. of taxa
C1	0% 0-2 m 20% 10-12 m 40% 24-26 m 40% 48-50 m	100% 10d	Anthozoa, Crinoidea
C2	0% 0-2 m 20% 10-12m 40% 24-26 m 40% 48-50 m	100% 30 d	Ophiurida, *Luidia sarsi* Paguridae, Pisidia sp. *Limanda limanda*
C3	10% 0-2 m 40% 10-12m 40% 24-26 m 10% 48-50 m	100% 30 d	Echinoida, Spionida, *Sabella* sp. *Nephrops norvegicus* *Corystes*
C4	10% 0-2 m 40% 10-12m 40% 24-26 m 10% 48-50 m	100% 60 d	Artica islandica, *Cancer pagurus,* Gadidae spp.
C5	40% 0-2 m 30% 10-12m 20% 24-26 m 10% 48-50 m	100% 30 d	*Calocaris macandrea.* *Liocarcinus navigator,* *Platichtys flesus*

Fig. 13. Model results - optimal networks for deep bottom larval types. Results from the analyses using eigenvalue perturbation theory (EPT) to identify the best grid cells for optimum networks in regards of larval connectivity for the 5 deep bottom larval types assessed for deep hard bottom habitats in the study domain. Red to blue color denotes high to low rank of areas.

Multispecies networks and comparison with existing MPAs

To identify the optimum networks of MPAs for benthic communities we used the EPT-method on the combined connectivity matrices from shallow (B1–5) or deep (C1–5) larval types in 4 different habitat scenarios (all shallow and deep areas, and shallow and deep hard bottom habitats; Fig. 14). The total area of selected MPAs was chosen to be of equal size as the total area of existing MPAs of each habitat type in the study area.

Shallow benthic communities. Including all shallow (1–20 m) areas in the model domain as potential habitat for the assessed larval types (B1–5), the EPT-method selected a network with a high number of sites outside the study area in the Danish straits and southwestern part of the Baltic Sea, and along the west coast of Jutland in the North Sea (Fig. 14a). Within the study area (Kattegat and Skagerrak and the Danish Straits), network sites were concentrated in the Danish Straits, along the coastline in western Kattegat, the large bays *Skälderviken* and *Laholmsbukten* in southeastern Kattegat, and 4 fjord-areas in the central part of the Swedish west coast (*Askimfjord, Nordre Älvs fjord, Hakefjord* and *Stigfjord*). In addition, a few MPA-sites were also selected in the central shallow part of Kattegat, along the northern coast of Jutland and eastern and western end of the south coast of Norway. No sites were selected along the central part of the Swedish Kattegat coast, or along the Swedish NW coast north of Stigfjorden (Fig. 14a).

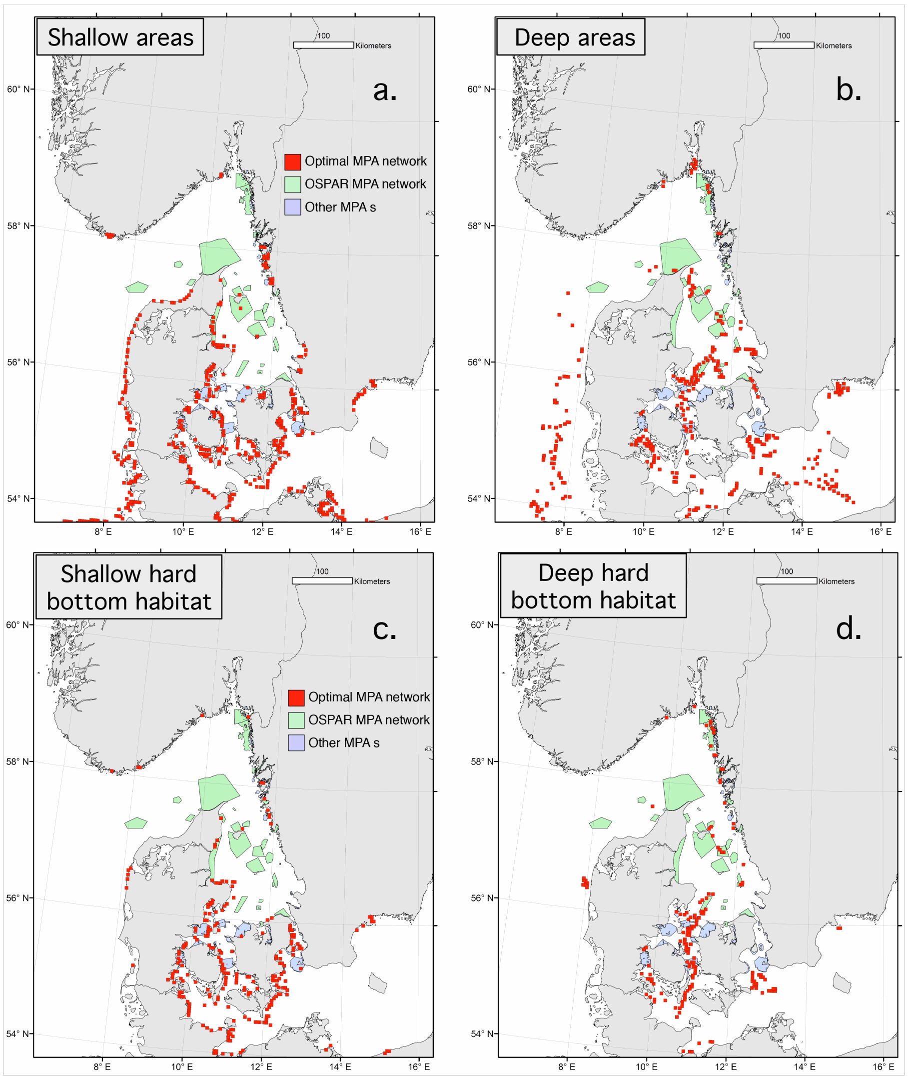


Fig. 14. Model results - Optimum networks for multispecies communities in 4 different habitats. Results from analyses using eigenvalue perturbation theory (EPT) to identify the optimum networks for the combined connectivity of 5 different larval types for shallow (1–20 m) or deep (21–100 m) benthic communities, using the same total area in the network as the combined area of the real world OSPAR-MPAs and other MPAs in the study region. Optimal networks for (a) shallow areas (all habitats), (b) deep areas (all habitats), (c) shallow hard bottom habitats, and (d) deep hard bottom habitats. The location of OSPAR-MPAs and other types of MPAs are shown on the map.

Comparing the EPT-selected sites with existing MPAs, a high number of selected sites were located within the OSPAR-MPA *Ålborg bugd* in western Kattegat and the MPAs *Nordre älvs estuarium* and *Stigfjorden* on the central parts of the Swedish west coast (Fig. 14a, 5). Sites were also selected within the OPSAR-MPAs around the islands *Læsø* and *Anholt* in the central part of Kattegat, indicated that these shallow areas may constitute important stepping-stones in the network. In the Öresund strait, sites were selected within the MPAs *Saltholm*, *Vestamager*, *Falsterbohalvön*, and *Stevns rev*. Many sites were also selected within the MPAs around the Little and Great Belt, in particular in *Lillebælt, Horsens fjord* and around *Odense fjord* (Fig. 14a, 5). In addition, a high number of selected sites were found within Natura 2000 MPAs in Danish and German part of the Baltic Sea (not shown in Fig. 5), indicating that these MPAs may also be important for a MPA-network for shallow benthic communities in the study area, at least for species that can tolerate the lower salinities in this area.

Looking at areas that the EPT-method selected for a MPA-network, but that are presently not included in any MPA, a high number of selected sites were found in the northern part of *Aarhus bugd* southeastern part of *Ålborg bugd* in western Kattegat, along the western side of the Öresund strait, in the *Laholms bay* and *Askimfjord* in eastern Kattegat, *Vårøyfjorden* close to Mandal in southern Norway, and along the coast in *Jammerbugten*, east of Hanstholm in northern Jutland (Fig. 14a). Based on the model result of connectivity, these areas could be considered to be included in a MPA-network for shallow benthic communities within the study area.

Shallow hard bottom communities. The optimum MPA-network for communities living on hard bottoms above 20 m depth showed slightly different patterns, as sites lacking hard substrates (e.g. *Skälderviken*, *Laholmsbukten*, areas in *Ålborg bugd*, and the coastline of northwestern Jutland) were no longer selected. However, the general pattern of the network was comparable with similar, but fewer sites selected in areas with shallow hard bottom substrates. In northern Skagerrak where rocky habitats are abundant along the coast, the location of the few selected sites shifted, and one site was now found in the Norwegian MPA *Ytre Hvaler* (Fig. 14b).

Deep benthic communities. The optimum MPA-network for communities living between 20–100 m depth on all types of substrates differed significantly from the optimum network for shallow communities. As for shallow communities, a high number of selected sites were found outside the study area, but now on deeper bottoms in the Danish and German part of the Baltic Sea and west of Jutland in the North Sea. In western part of Kattegat and of the Danish straits, which are dominated by areas shallower than 20 m, very few sites were selected. Instead, the selected MPAs in western Kattegat were concentrated in the deeper channels of the Great Belt and in the channels continuing northeast towards the *Schultz shallow* and west towards *Århus bugt* (Fig. 14c). According to the multispecies source-sink analyses of deep larval types, these channels are important as both sink and sources for deep benthic communities in western and eastern Kattegat (Fig. 11k,l,p,q) indicating that the channels concentrate the deep drifting larvae, increasing connectivity and their value in a MPA-network. In eastern Kattegat that has a average depth >20 m, a concentration of MPA-sites were found around *Lysegrund*, in the norther part of Öresund strait, outside *Hallands Väderö* towards *Stora Middlegrund*, and between *Anholt* and *Fladen*. In northern Kattegat, the selected sites were found along the Danish coast between Læsø and Skagen (Fig. 14c, 5). Interestingly, no MPA-sites were selected along the Swedish west coast in Kattegat north of *Hallands Väderö*, and very few sites were found in western Skagerrak (north of Jutland), although the latter constitutes an important source area for Kattegat and Skagerrak (Fig. 11). Along the NW coast of Sweden, a few sites were found outside the *Gullmarsfjord* and in the *Koster* archipelago. Along the south coast of Norway, the sites were concentrated at the mouth of the Oslo fjord and the *Langesundsfjord* (Fig. 14c).

Comparing the EPT-sites with existing MPAs, selected sites were found within the OSPAR-MPAs *Kosterfjorden-Väderöfjorden* and *Gullmarsfjorden* along the Swedish NW coast. In central Kattegat, many sites were found within the OSPAR-MPA *Kims Top* close to *Lilla Middlegrund,* but also within the OSPAR-MPAs *Læsø Trindel, Anholt, Morups bank, Stora Middlegrund, Lysegrund* and *Hesselø* (Fig. 14c, 5). In western Kattegat, a high number of MPAs were found concentrated around the shallower OSPAR-MPA *Schultz og Hastens grund*, but few inside the MPA. Similarly, most of the Natura 2000 MPAs in the Danish straits are located at shallower depth than 20 m so that the selected sites were located just outside the existing MPAs (e.g. *Begtrup vig and Mejl Flak, Stavns fjord, Munkegrunde, Hatterbarn,* and *Lillebælt*). The Natura 2000 MPA *Centrale Storebælt* is a noteworthy exception, including large areas of depth >20 m, and a high number of selected MPA sites (Fig. 14c, 5). This MPA may play a key role for a MPA-network for deep benthic communities in the Danish straits and the Kattegat area.

Using the model results to indentify unprotected areas to include in a MPA-network, the EPT-method suggested that the mentioned deeper channels in the Great Belt and western Kattegat play a key role in a network for deep benthic communities in the study area. The deeper northern part of the Öresund strait, and the area northwest of the *Hallands Väderö* in southeastern Kattegat also appear to play an important part in such a network. In northwestern Kattegat, the deeper area between Læsø and Skagen received a high number of sites. This area constitute both a source and a sink to all other regions in the study area (Fig. 11) indicating that it constitutes an important stepping stone for sites further north in the network. Along the Norwegian coast, the area outside the Oslo fjord and the *Langesundsfjord* appear to be key areas for the MPA-network in northern Skagerrak (Fig. 14c).

Deep hard bottom communities. The optimum MPA-network for communities living on hard bottoms at 20–100 m depth showed slightly different pattern compared to the network for communities living on all types of deep bottoms. The selected sites in the Great Belt and southwestern Kattegat were similar since hard substrate was common in these areas, according to the model data. However, due to lack of hard bottoms (Fig. 4), no sites were selected in Öresund strait, outside the *Hallands Väderö,* and between between Læsø and Skagen (Fig. 14d). This shift in distribution of possible sites for the network resulted in a shift in the optimal network so that the areas around around *Lysegrund* and *Anholt* were no longer selected, although hard bottom substrates were available in these areas. Instead, a number of new sites were included along the Swedish west coast in both Kattegat and Skagerrak, effectively doubling the number of sites in this area, despite the fact that the number of potential habitats in the area were reduced in half compared when all deep habitats were available (Fig. 14d, 4). This result demonstrates how sites for an optimum network in one area may change depending on the available sites in another area.

Comparing the EPT-selected sites for deep hard bottom communities with existing MPAs resulted in the same MPAs as for all deep bottoms, except that sites within *Hesselø*, *Lysegrund* and *Anholt* was no longer selected, and that sites within the Natura 2000 MPAs *Härmanö* and *Måseskär*, and more sites within *Kosterfjorden-Väderöfjorden* were selected. The results also suggest that area west of *Kungsbackafjorden* and *Nordre älvs estuarium,* and north of *Åbyfjorden* could be considered as new areas for MPAs for an optimal network for deep hard bottom communities (but see chapter 3.4 about the limitations of the habitat data).

3.3.2.4 Assessing the EPT-results with metapopulation models

To evaluate if the grid cells identified by the EPT-method really represented the best MPA-network with respect to larval connectivity, we carried out metapopulation modeling comparing the protective effects of the EPT-selected MPA-network during periods of low population densities with the effect of a randomly selected network and with the real-world MPA-networks. The results confirmed that the EPT-method did select networks that provided substantially better protection to the benthic communities compared to randomly selected networks and the existing MPA-networks for all habitat scenarios, resulting in several times larger metapopulation communities.

All shallow and deep habitats

Assessing all types of shallow bottoms and multispecies connectivities, the EPT-selected network resulted in metapopulations that were 2.6–2.7 times larger compared to a random network, and 2.6 and 3.1 times larger when compared to network of existing OSPAR-MPAs and all types of MPAs of equal size, respectively (Fig. 15a). For all types of deep bottoms communities, the difference was slightly smaller, where the EPT-network resulted in 90–98 %

larger populations compared to random networks, and 76–78 % larger populations compared to real world MPAs of equal size (Fig. 15d). In comparison, the real world MPAs provided only marginally larger populations, 0–13 % larger than the random networks of the same size (Fig. 15ab).

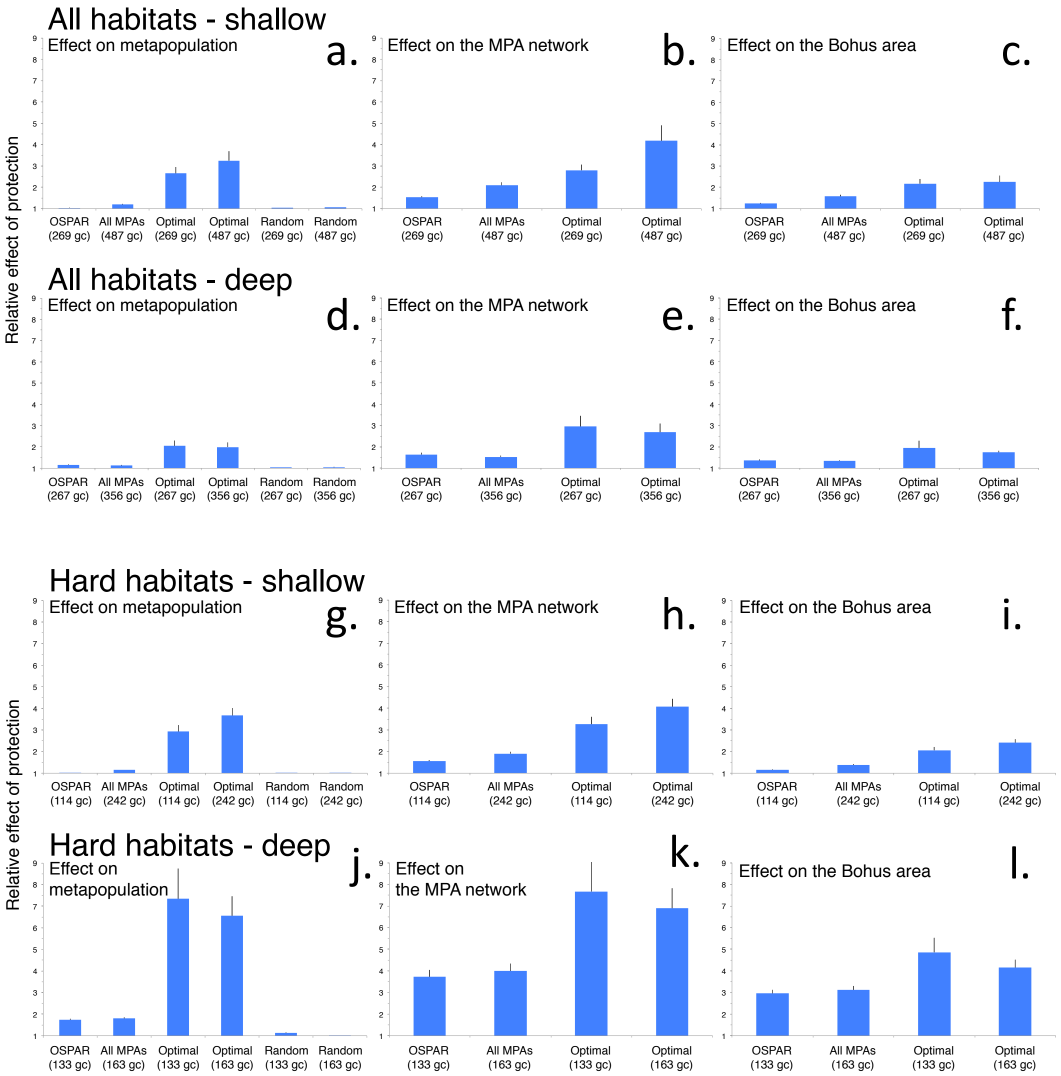


Fig. 15. Comparison of the relative protective effects on modeled metapopulations of the assessed multispecies communities from real word MPA-networks (OSPAR-MPAs and all MPAs), networks selected with the EPT-method (Optimal), and randomly selected networks (Random) in 4 different habitat types: all shallow habitats (all substrates included from 1-20 m; a–c), all deep habitats (all substrates included from 21–100 m; d–f), shallow hard habitats (g–i) and deep hard habitats (j–k). Within each habitat type, the relative protective effects was compared in 3 different ways: (1) on the metapopulations within the whole study domain (a,d,g,j), (2) only on the metapopulations within the MPA-network (b,e,h,k), and (3) on all metapopulations within the eastern Skagerrak region (NW coast of Sweden or Bohus; c,f,i,l). All comparisons between real world-, EPT- and random networks were done for the same area (same number of grid cells in the model), which is depicted underneath each bar.

In these network comparisons, habitats also outside the MPAs were included in the network, but the populations within the MPAs were given 20 % higher reproduction in the metapopulation models to simulate the protective effect of the MPAs. An alternative assessment is to treat all habitats outside the MPAs as non-productive, and only assess the metapopulation size within the MPAs. Although this is less realistic since most of the living communities are found outside the MPAs, it is the approach used in the recent assessments of the coherence of the OSPAR and HELCOM MPA-networks (HELCOM 2010, OSPAR 2011, Johnson et al. 2013). Also in this comparison, the EPT-network produced larger metapopulation sizes (76–100 % larger) compared to the existing MPA-networks (Fig. 15b,e). Thus, also when only considering the connectivity between the MPAs, the EPT-method selected a better network.

One of the unexpected results in the study was that the EPT-method selected most sites for the optimum MPA-networks in southwestern Kattegat and the Danish straits within the study area for all habitats scenarios, and very few sites along the NW coast of Sweden, particularly for shallow bottom communities (Fig. 14). Since the NW coast of Sweden (region eastern Skagerrak) have a large number of OSPAR-MPAs, Natura 2000 MPAs and Nature Reserves (Fig. 15; Table A1.4, A1.5 in Appendix A), it would be interesting to compare protection afforded by the EPT-network with the existing networks for this region. Surprisingly, the EPT-network resulted in 76–83 % larger populations for shallow bottom communities, and 44 % and 83 % larger populations in deep bottom communities in the NW coast of Sweden, compared to existing networks of OSPAR and all types of MPAs, respectively of equal size (Fig. 15c,f). Thus, although the existing network of MPAs has a much larger area and higher proportion of MPAs within the eastern Skagerrak region than the EPT-network, the latter provided better protection to the populations along the NW coast of Sweden. These results suggest that it can be better to place MPAs outside the targeted for protection if the circulation creates asymmetric connectivities, such as in the Kattegat-Skagerrak area.

Shallow and deep hard bottoms

The difference between the EPT-selected network and realword networks was even larger when assessing shallow and deep hard bottom communities. For shallow hard bottoms, the EPT-selected network resulted in 3.0–3.8 times larger populations when compared to a random network and 3.0 and 3.3 times larger populations when compared to network of existing OSPAR-MPAs and all types of MPAs of equal size, respectively (Fig. 15g). For deep hard bottom communities the EPT-network resulted in 7.0–7.1 and 4.5 and 3.8 times larger populations compared to random networks and compared to OSPAR-MPAs and all types of MPAs of equal size, respectively (Fig. 15j). The larger difference between EPT and randomly selected networks for hard bottom communities may indicate that the EPT-method is more important when the available habitat is restricted making the correct choice more important. Comparing only the metapopulationsizes within the MPA-network, the EPT-network produced 2.2 and 2.3 times larger metapopulations on shallow hard bottoms, and 2.1 and 3.9 times larger populations in deep hard bottom communites compared to the networks in OSPAR and all types of MPAs, respectively (Fig. 15h,k). Similarly to the analysis of all habitats, the EPT-network for hard bottom communities resulted in 35–83 % larger metapopulations in the NW coast of Sweden, compared to real world MPAs located in the region (Fig. 15c,f).

Thus, the EPT-methods managed to produce a MPA-network that provided better protection to benthic communities of all habitat types, and for all parts of the study area, than did the existing MPA-networks, which perform no better than a randomly selected network. These results suggest that the existing MPA-networks in Kattegat and Skagerrak could be improved substantially without increasing their total size, but by carefully selecting the locations that enhance larval connectivity in the network, the population size of targeted communities could increase many times during periods of low abundance.

3.4 LIMITATIONS OF THE STUDY

The present study should be seen as a first test of how modeled data of larval dispersal could be used to assess the effect of larval connectivity for the ecological coherence of MPA networks in the Kattegat-Skagerrak area. The study has several limitations and the results should not be viewed as a blueprint of an optimum design of MPA-networks in the area.

The large spatial scale of the oceanographic model likely leads to an underestimate of the connectivity within a topographically complex coastal zone. Thus the results indicating very low connectivity within coastal Skagerrak should be interpreted with caution. The poor quality of the data of hard bottom habitats used in the model has likely resulted in a serious overestimate of their distribution, and the analysis regarding connectivity between these habitats should be viewed as an exercise rather than representing true distribution and connectivity. Moreover, the study only assessed the importance of larval connectivity (and indirectly the effect of MPA-size and replication) for the ecological coherence of the MPA-network, and did not include migration of adult stages or any aspects of habitat quality or distribution of species (information that is presently not available). Thus, if other criteria had been included, a different optimal network could have been found. Also, the simulation did not include physiological barriers to dispersal and survival, such as the low salinity in the Danish straits and in particular the southwestern part of the Baltic Sea. Since these areas were included in the networks, although the low salinity would not allow echinoderms and many other species of deep bottom communities to survive or reproduce, the results should be interpreted with caution for these animals.

Still, the oceanographic model is state-of-the-art, and the larval traits simulations are based on a unique set of empirical data providing the best possible assessment to day of larval dispersal and connectivity in the study area. The large-scale dispersal patterns between deeper areas away from the coast do not suffer from the mentioned limitations and therefore provides a better description of the true larval connectivity. Thus, the general results of areas of high and low connectivity and their implications for designs of MPA-networks may be directly of use for managers.

3.5 DISCUSSION AND CONCLUSIONS

3.5.1 Comparison with previous approaches for assessing connectivity of MPA-networks

In earlier evaluations of *ecological coherence* of MPA-networks in OSPAR and HELCOM, connectivity has been assessed on the basis of general fixed connection distances between MPAs (HELCOM 2010, OSPAR 2011, OSPAR 2013). The present study differs in a number of critical ways from these attempts that we argue improve the assessment of larval connectivity.

First, we have not only assessed connectivity between MPA-areas, but have included all areas that may harbor the type of benthic community being assessed, based on the best available information of habitat distribution. Since the benthic communities targeted in the MPAs are mainly found outside the MPA-network, this approach provide a much more realistic assessment of the connectivity within the metapopulations than simply measuring connectivity between MPAs. In the present study we simulated the effect of the MPA-protection by giving populations within MPAs a higher rate of reproduction compared to populations outside the network. This, we believe, simulate the protective effect of MPAs in more realistic way than excluding reproduction all together outside the MPAs. Pilot studies showed that varying the effect on reproduction within the MPAs had little effect on the comparison between networks.

Second, we made an attempt to include information of habitat and species distribution in the connectivity analyses, which has not been included in previous assessments of MPA-networks in OSPAR and HELCOM. However, due to the acute lack of data, we have only approximated the distribution in two different ways. First we separated all areas in the model according to if they were located above or below 20 m depth, to take into account the estuarine conditions in the study area and pulses of fresh water affecting the benthic communities down to 20 m depth, which also approximate the photic zone in the study area. We also used modeled data of the distribution of hard substrate in the study area to include an assessment of shallow and deep hard bottom communities. However, this data is not very accurate and this analysis should mainly be viewed as an exercise.

Third, we included the effect of larval traits, based on empirical data obtained in the study area, and its interaction with local oceanographic circulation to model the connectivity for a large number of larval types for all areas of the study domain. The results demonstrated that larval dispersal distances and connectivity were strongly affected by the drift depth and the pelagic larval period, as well as by the area from where the larvae had been released in the model. Virtual larvae with different larval traits released from the same area differed >10 times in average dispersal distance, and for the same larval type the average dispersal distance varied >100x between different areas of the Kattegat and Skagerrak. These strong regional differences, and large effects of larval traits demonstrate that it is not very useful to assess connectivity within and between MPAs with a fixed distance, as has been the praxis so far in evaluations of ecological coherence of MPA-networks (HELCOM 2010, OSPAR 2011, OSPAR 2013). The average modeled dispersal distances varied between approximately 10–140 km, which are similar to previous estimates in the literature (Shanks et al. 2003, Palumbi 2004, Corell et al. 2012), but much smaller than the fixed dispersal distances used to assess connectivity in near-shore and offshore areas in an earlier OSPAR assessment (250 and 500 km, respectively; OSPAR 2008) suggesting that the latter estimates are not realistic.

Lastly, we used the connectivity matrices for groups of larval types and a new method using *eigenvalue perturbation theory* (EPT) to identify the optimum network of MPAs with respect to the larval connectivity for whole benthic communities, and subsequently evaluated the results using metapopulation model based on the connectivity matrices. This is the first time connectivity matrices have been used to identify the best MPA-network, and the first time several organisms with different dispersal strategies have been taken into account simultaneously. In previous evaluations, dispersal and connectivity has at best been assessed for one species at the time. However, the goals of OSPAR and HELCOME MPA-networks are to protect biodiversity and whole communities of plants and animals. The present study is first to provide a model tool for finding such *consensus networks.* Although this is the first attempt to assess this new method (more studies and scientific evaluation are needed before it can be applied as a management tool), the results presented here appear to be robust and we encourage further studies with this method. A scientific article presenting the EPT-method for multiple species is presently being prepared (Jonsson et al. *in prep.*).

3.5.2 Using the results for management of MPAs in Kattegat and Skagerrak

Although the present model study has several limitations (see chapter 3.4), it still produced results that may be of direct use for managers of MPAs in the study area. Considering that the average diameter of an OSPAR-MPA and other types of MPAs in the study area are approximately 18 and 7 km, respectively, and that all larval types dispersed >20 km in most areas, most MPAs in Kattegat and Skagerrak are far to small to allow self-recruitment (i.e.

settlement of larvae within the same MPA as they have been released). However, there was large regional variation in dispersal distances. For example, in the shallow western part of Kattegat and the Danish Straits, dispersal was in general lower, particularly for deep-drifting larvae, which may allow self-recruitment in the larger MPAs located there (e.g. *Ålborg bugd, Horsens fjord, Lillebælt*; Fig. 5). In contrast, the large dispersal distances found for all larval types along the west coast of Sweden and most areas of Skagerrak (outside fjords and the coastal archipelagos) make self-recruitment highly unlikely there. Maps such as Fig. 9 and 10, generated in this study may provide useful in determining the potential for self-recruitment within MPAs in different areas.

The large dispersal distances indicated in the model study suggest that a functional MPA-management in the study area must depend on the larval connectivity between a network MPAs and other areas. In designing such a network it is important to take into account the unique estuarine circulation in Kattegat and Skagerrak resulting in a transport of surface water along the Swedish and Norwegian coasts, and out of the study area. As discussed in chapter 3.3.2.4, this circulation has large effects on the transportation of larvae drifting on different depth, resulting connectivities and optimum MPA-networks that differ between larval types and depend on the distribution of habitats. It is therefore critical to determine the larval traits and habitat distribution of the targeted organisms when designing the MPA-network. Interestingly, the model results suggest that the optimum MPA-networks will produce larger populations of benthic organisms along the NW coast of Sweden than the existing MPA-network, although the latter has a much higher proportion of MPAs within this area. This result indicates that managers need to consider the possibility that it may be more efficient to place MPAs outside the area targeted for conservation (even in a different country).

Figures 12–14 summaries the model results of the optimum MPA-networks for different larval types and communities on different habitats in Kattegat and Skagerrak. Taking the limitations of the study into account, and interpreting with caution, these maps may provide some guidance in identifying the most valuable areas to include in a MPA-network for a target organism or community. For example, by using table A1.3 (Appendix A) to identify the larval type(s) and habitat for an organism/community on *OSPARs list of threatened and/or declining species* (e.g. the stone corall *Caryophyllia smithii*; larval type C2; habitat: deep hard bottoms), the optimal MPA-network can be found by choosing the corresponding map (Fig. 13, C2). Using figure 5 and Table A1.4 and A1.5 (Appendix A) showing the location and information about existing MPAs in the study area, key areas for larval connectivity that need further protection can be identified to possibly include in the existing network (see chapter 3.3.2.4 for examples). As better data on the distribution of hard and soft sediment bottoms becomes available, the model could be rerun and provide better estimates of the optimal MPA-network for different benthic communities.

3.5.3 Conclusions

This study provides a demonstration of how oceanographic modeling informed by biological traits of larvae could be used to obtain detailed description of the dispersal and connectivity of larval stages of selected benthic organisms in the Kattegat and Skagerrak region. It also demonstrates how a new theoretical method could be used to identify the optimum MPA-network for different species as well as for whole communities. The results suggest that the present OSPAR-MPA network in the Kattegat and Skagerrak area does not have the best design in regards of larval connectivity. Most MPAs are too small to allow self-recruitment for the targeted organisms, and they are not placed in the best locations for a functional network. The study suggests that the existing MPA-networks could be improved substantially without increasing their total size, but by carefully selecting the locations that enhance larval connectivity in the network. This would increase the larval supply and population size of the benthic communities, particularly during periods of low abundance, making them more resilient to stressors. While taking the limitations of the study into account, the presented results provide a number of suggestions of how connectivity of the network could be improved by including new MPAs into the network. We find the model methods presented her promising as new tools to assess key criteria for the evaluation of ecological coherence of MPA-networks. We recommend that efforts are made to improve the data on habitat and species distribution in the OSPAR region, which are key for the assessment of MPA-networks.

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APPENDIX A

Table A1.1. Summary of invertebrate larval traits from Skagerrak and Kattegat based on results from plankton surveys and the literature. The table shows the total number of samples (n), the total number of samples in which the taxa was encountered (N), the average density, depth distribution, and seasonal larval occurrence (all based on the plankton survey), and pelagic larval duration (PLD), and adult distribution (based on the literature) for a total of 80 different larval taxa and stages. Superscript numbers indicate references: Hansson 2007 (1), O'Connor et al. 2007 (2), Pires et al. 2008 (3), Rees 2001 (4), Shanks 2009 (5), www.marlin.ac.uk (6), Munk et al. 2005 (7).

					Density		Depth distribution (m)							Adult habitat		
					(no. 100 m-3)		0-10	10-30	0-10	0-10	PLD	Larval	Larval	Depth	Substrate	Distribution
Phylum /Class	Order/Family	New Species/stage	n	N	Ave	SE	%	%	Dag (%)	Natt (%)	(d)	Occurrence	Peak	(m)		
Bivalvia																
		Bivalve veliger larva	172	108	723.2	89.8	9%	86%	9%	8%	16-39 ^{2}	Jun-Aug	Jul	Sp.d	Sp.d	
Gastropoda																
		Gastropod veliger larva	172	128	686.0	51.5	22%	57%	14%	23%	25-42 ^{2}	All year	Aug	Sp.d	Sp.d	
		Nudibranchia (cf.)	172	14	17.6	0.4	46%	54%	37%	63%		Jul-Dec	Aug	> 350	H	Katt-Skag
Polychaeta		Trocophore larva	172	67	112.6	14.5	48%	37%	6%	67%	20-40 ^{2}	All year	Jul	Sp.d	Sp.d	
	Spionida	Spionid sp.	172	21	100.4	3.4	22%	72%	22%	0%	20-40 ^{2}	All year	Jan	Sp.d	Sp.d	
		Poecilochaetidae	172	12	284.3	5.7	0%	100%	0%	0%	20-40 ^{2}	Jul	Jul	Sp.d	Sp.d	
	Phyllodocia	Polynoidae	172	14	77.3	2.2	55%	41%	58%	0%	20-40 ^{2}	Mar-Jul	Mar	Sp.d	Sp.d	
Phoronida																
		Phoronid larva	172	14	14.8	0.3	32%	55%	41%	17%	11-30 ^{6}	Aug-Dec	Aug	0-10; 9-50	S,M,H	Katt-Skag
Bryozoa																
		Cyphonautes larva	172	27	467.5	21.0	54%	43%	51%	56%	< 1 ^{5}	Aug-Apr	Dec	0–42 ^{6}	H ^{6}	
Cnidaria																
		Cnidaria	172	3	18.2	0.2	0%	100%	0%	NaN	< 1 ^{5}	Mar-Apr	Mar	< 10 ^{6}	Sp.d	
Echinodermata		Echinodermata spp.	172	21	388.5	20.1	2%	98%	3%	1%		Aug	Aug			
	Ophiuroidea/Echinodea	Pluteus larva	172	15	1927.0	40.6	22%	78%	3%	30%		Jul	Jul			
	Ophiurida (~11 spp.)	Ophiurid juvenile	172	30	618.6	51.2	1%	99%	0%	19%		Jul	Jul	< 350	S,M,G ^{6}	Katt-Skag
	Echinoida (3-4 spp.)	Echinoid juvenile	172	18	71.4	2.0	39%	61%	34%	57%	30-60 ^{6}	Jun-Aug	Jul	0-100; >1200	S,H	Katt-Skag
	Asteroidea	Bipinnaria larva	172	16	64.6	3.2	78%	21%	81%	39%	30-60 ^{8}	Jun-Nov	Jun	< 900	S,M,H	Katt-Skag
		Brachiolaria larva	172	14	45.1	0.9	53%	47%	52%	55%	40-50 ^{8}	Jul	Jul	< 900	S,M,H	Katt-Skag
	Luidiidae (2 sp.)	Luidia sarsi	172	14	11.2	0.2	9%	90%	14%	0%	30-60 ^{6}	Oct-Apr	Mar	10-1300	S,M	Katt-Skag
Crustacea																
	Cirripeda															
	Balanidae (5-7 spp.)	Naplius larva	172	77	211.8	12.8	28%	65%	32%	14%	14-28 ^{5}	All year	Jun	0-6; 60-300	H ^{6}	SW BS-Skag
		Cyprid larva	172	101	111.2	8.3	28%	63%	28%	26%	14-28 ^{5}	All year	Jul			
	Caridea	Caridea spp. Z	330	122	18.1	2.3	24%	67%	20%	33%	30-60 ^{6}	All year	Jul	-	-	
	Paelmonidae (4 spp.)	Palaemon sp. Z1-2	330	24	19.2	0.5	8%	92%	2%	17%	30-60 ^{6}	Jul-Aug	Jul	0-10 (40)	M,H	SW BS-Skag
		Palaemon sp. Z3-5	330	74	3.9	0.2	80%	18%	66%	97%	30-60 ^{6}	Jul-Aug	Jul			
		Palaemon sp. PL	330	9	0.3	0.0	43%	20%	41%	46%	30-60 ^{6}	Jul-Aug	Jul			
	Crangonidae (2 spp.)	Crangon sp. Z1-3	330	42	2.7	0.3	8%	89%	5%	33%	30-180 ^{6}	Jul-Nov	Aug	0-22, 30-250	S,M ^{6}	SW BS-Skag
		Crangon sp. Z4-5	330	39	1.2	0.0	43%	28%	45%	59%	30-180 ^{6}	Jul-Nov	Aug			
		Crangon sp. PL	330	85	4.0	0.3	53%	31%	35%	62%	30-180 ^{6}	Jul-Nov	Aug			
		Philicheras bispinosus Z	330	8	3.1	0.0	0%	85%	0%	0%		Mar-Jul	Jun			
	Pandalidae (6 sp.)	Pand ZI-V	330	8	19.1	0.2	75%	25%	56%	93%	30-180 ^{6}	Jul	Jul	20-550	S,M,H	Katt-Skag
		Pandalina brevirostus Z	330	2	0.2	0.0	35%	65%	35%	NaN	30-60 ^{6}	Jul	Jul	10-50	S,H	Katt-Skag
	Alphaeidae (1 sp.)	Athanas nitescens (cf.) PL	330	4	0.6	0.0	94%	6%	74%	100%	~ 4 ^{3}	Jul	Jul	1-13	S,H	Katt-Skag
		Alphaeid Z	330	2	0.5	0.0	72%	28%	0%	100%	~ 4 ^{3}	Jul	Jul	1-13	S,H	Katt-Skag
	Hippolythidae(~6 sp.)	Hippolythid Z	330	11	76.7	1.0	13%	87%	0%	20%	30-60 ^{6}	Jul	Jul	3-30; 30-300	S,M,H	Katt-Skag
	Callianassidae (1 sp.)	Callianassa sp. Z	330	12	18.9	0.3	6%	84%	10%	0%	30-60 ^{6}	Jul-Sep	Sep	30-60	M,S	Skag
	Thalassinidea															
	Upogeviidae (2 sp.)	Upogebia sp. Z	330	8	2.7	0.0	18%	66%	0%	47%	11-30 ^{6}	Jun-Aug	jul	8-20	S,H	Katt-Skag
		Upogebia sp. PL	330	30	0.7	0.0	7%	70%	8%	8%		Jun-Aug	jul			
	Axiidae (2 sp.)	Calocaris sp. Z	330	54	112.6	5.7	44%	40%	2%	12%		Jul-Aug	Aug	12-1070	M	Katt-Skag
	Astacidae															
	Nephrodidae (2 sp.)	Nephrops norvegicus Z1-2	330	38	1.4	0.1	19%	77%	20%	8%	30-60 ^{6}	Mar-Oct	Jul	27-300	S,M	Katt-Skag
		Nephrops norvegicus Z3-5	330	22	1.4	0.0	12%	85%	12%	0%		Mar-Oct	Jul			
		Homarus gammarus Z1	330	1	0.2	-	100%	0%	100%	NaN	15-35 ^{6}	Jul	Jul	3- >30	S,H	Katt-Skag
	Anomura															
	Paguridae (5-7 sp.)	Pagurid Z1-5	330	46	12.3	0.4	5%	91%	6%	0%	11-30 ^{6}	All year	Jun	0-470	S,M,H	Katt-Skag
		Pagurid PL	330	30	0.9	0.0	4%	90%	1%	29%		All year	Jun			
	Galatheidae (9 spp.)	Galathea sp. Z	330	42	24.3	0.8	13%	73%	4%	0%	180 ^{6}	Mar-Sep	Aug	10-110	S,H	Katt-Skag
		Galathea sp. PL	330	4	0.6	0.0	70%	8%	84%	0%		Mar-Sep	Aug			
		Munidopsis sp. PL	330	24	0.5	0.0	49%	51%	0%	53%		Jul	Jul			
	Porcellanidae (1 sp.)	Pisidia longicornis (cf.) Z	330	45	28.9	0.9	9%	81%	0%	0%	30 ^{6}	Apr-Nov	Jul	0-70	H	Katt-Skag
		Pisidia longicornis (cf.) PL	132	65	1.4	0.1	10%	63%	1%	27%		Apr-Nov	Jul			
	Brachiura															
	Portunidae (7- 11 spp.)	Carcinus maenas Z1-2	330	100	21.4	1.3	30%	19%	8%	27%	40 ^{6}	Jun-Aug	Aug	0-40	S,M,H	Katt-Skag
		Carcinus maenas Z3-4	330	115	27.8	1.9	30%	30%	19%	29%		Jun-Aug	Aug			
		Carcinus maenas M	330	172	17.1	1.7	24%	69%	14%	36%		Jun-Aug	Aug			
		Liocarcinus navigator (cf.) Z1-2	330	29	14.9	0.3	28%	71%	27%	30%		All year	Aug	1-100; 1-450	S,M,H	Katt-Skag
		Liocarcinus navigator (cf.) Z3-5	132	18	19.2	0.6	85%	15%	29%	100%		All year	Aug			
		Liocarcinus navigator (cf.) M	330	143	1.5	0.1	67%	29%	63%	67%		All year	Aug			
		Liocarcinus depurator (cf.) Z1-2	330	17	20.2	0.5	10%	90%	6%	22%		Jul-Oct	Jul	1-100; 1-450	S,M,H	Katt-Skag
		Liocarcinus depurator (cf.) Z3-5	132	14	13.3	0.3	21%	79%	1%	34%		Jul-Oct	Jul			
		Liocarcinus depurator (cf.) M	132	61	1.0	0.1	22%	68%	5%	37%		Jul-Oct	Jul			
		Liocarcinus sp. M	330	89	2.3	0.1	36%	57%	31%	40%		Jul-Oct	Jul	0-450 ^{6}	S,M ^{6}	
		Necora puber (cf.) Z1-4	330	5	31.7	0.4	26%	74%	19%	84%	30-60 ^{6}	Jun-Sep	Jun	> 60	H	Katt-Skag
		Necora puber (cf.) M	132	8	10.5	0.3	11%	83%	10%	100%		Jun-Sep	Jun			
		Portunid sp. M	330	45	2.2	0.1	25%	58%	22%	40%		Jul-Aug	Jul	1-450	S,M,H	Katt-Skag
		Portunid sp. Juvenile	132	26	1.4	0.1	11%	84%	19%	10%		Jul-Aug	Jul			
	Pirimelidae	Pirimela denticulata (cf.) Z	132	16	16.3	0.5	58%	42%	11%	76%		Jul-Aug	Aug	> 180 ^{6}	S,M,G ^{6}	Katt-Skag
	Cancridae (1 sp.)	Cancer pagurus Z1-5	330	22	31.7	0.9	36%	61%	38%	1%	30-144 ^{6}	Jun-Sep	Jul	1-50	S,M,H	Katt-Skag
		Cancer pagurus M	330	59	2.0	0.1	19%	57%	8%	33%		Jun-Sep	Jul			
	Thiidae (1 sp.)	Thia scutella (cf.) Z1-3	330	2	4.2	0.0	0%	100%	0%	NaN		Mar-Aug	Jan	> 30 ^{4}	S	Katt-Skag
	Corystidae (1 sp.)	Corystes cassivelaunus Z1-3	132	7	5.9	0.1	27%	73%	10%	100%	11-30 ^{6}	Mar-Aug	Jun	7-90	S,M	Katt-Skag
		Corystes cassivelaunus Z4-5	330	7	10.0	0.1	34%	56%	34%	NaN		Mar-Aug	Jun			
		Corystes cassivelaunus M	330	3	0.7	0.0	0%	12%	0%	0%		Mar-Aug	Jun			
	Atelecyclidae (1 sp.)	Atelecyclus rotundatus Z1-3	330	10	11.4	0.1	57%	43%	2%	73%		Jul-Aug	Jul	< 12	S	Katt-Skag
		Atelecyclus rotundatus Z4-5	132	12	8.2	0.2	34%	66%	21%	36%		Jul-Aug	Jul			
		Atelecyclus rotundatus M	132	1	0.1	-	0%	100%	NaN	0%		Jul-Aug	Jul			
	Majidae (8 sp.)	Hyas spp. Z1-2	132	3	16.2	0.2	0%	100%	0%	0%	30-180 ^{6}	Mar-Jul	Jul	3-50; 12-120	S,H	Sw BS-Skag
		Hyas spp. M	330	4	6.2	0.0	0%	100%	0%	NaN		Mar-Jul	Jul			
		Macropodia rostrata M	330	3	0.5	0.0	0%	90%	0%	0%	11-30 ^{6}	Jul	Jul	2-86	S,M,H	Katt-Skag
		Euronyme spp. (cf.) Z1-2	330	1	37.9	0.1	0%	100%	NaN	0%		Aug	Aug	12-40;12-120	S,H	Katt-Skag
		Euronyme spp. (cf.) M	330	12	0.5	0.0	4%	27%	0%	0%		Aug	Aug			
	Pinnotheridae (1 sp.)	Pinnotheres pisum (cf.) Z	330	1	5.5	-	0%	100%	NaN	0%		Aug	Aug	5-50	S,H	Katt-Skag
	Geryonidae (1 sp.)	Geryon trispinosus (cf.) Z1-3	132	6	12.4	0.2	25%	75%	0%	100%		Jul-Aug	Jul	-	-	
	Pilumnidae (~3 spp.)	Pilumnus hurtellus (cf.) Z1	132	1	4.8	-	100%	0%	100%	NaN	30-60 ^{6}	Sep	Sep	> 70 ^{6}	H ^{6}	Skag
		Pilumnus hurtellus (cf.) M	330	1	1.4	-	0%	100%	NaN	0%		Sep	Sep			
	Leucosidae (2-3 sp.)	*Ebalia* spp. Z1-4	330	16	2.9	0.1	2%	83%	0%	0%	30-60 ^{6}	Jul-Sep	Jul	12-60	S,H	Katt-Skag

Habitat legends denote type of habitat where species are found or an established preference. S=Sand, M=Mud, G=Gravel, H=Hard substrate, Sp.d= species dependent
All depth, distribution and substrate preferences are from reference no. 1 unless otherwise indicated.

Table A1.2. Summary of fish larval traits from Skagerrak and Kattegat based on results from plankton surveys and the literature. The table shows the total number of samples (n), the total number of samples in which the taxa was encountered (N), the average density, depth distribution, and seasonal larval occurrence (all based on the plankton survey), and pelagic larval duration (PLD), the spawning period, and adult distribution (based on the literature) for a total of 45 different larval taxa and stages. Information of spawning season is from Munk and Nielsen 2005, and information about PLD and habitat and depth distribution of adult dish is from Bording 1985.

					Density		Depth Distruibutions (m)					Seasonality			Adult	
					(no. 100 m-3)		0-10	10-30	0-10	0-10	PLD	Larval	Larval	Spawn Per.	Depth	Habitat
Order	**Family**	**Species/stage**	**n**	**N**	**Ave**	**SE**	**%**	**%**	**Day (%)**	**Night (%)**	**(d)**	**Occur.**	**Peak**	**Literature**	**(m)**	
Clupeiformes																
	Clupeidae	*Sprattus sprattus*	201	9	19.56	0.57	44%	56%	45%	0%		Mar-Aug	Mar	Jan-Jul	10-150	P
	Clupeidae < 10		201	68	7.46	0.87	38%	60%	39%	32%		Mar-Aug	Mar	Mar-May, Sep-Jan	> 300	P
	Clupeidae > 10		201	40	0.74	0.04	28%	70%	40%	20%		Mar-Aug	Mar	Mar-May, Sep-Jan	> 300	P
Gadiformes																
	Gadidae	*Gadus morhua*	201	5	6.78	0.09	39%	61%	39%	NaN	60-120	Mar-Apr	Apr	Jan-Jun, Oct-Dec	5-500	-
	Gadidae	*Merlangius merlangus*	201	2	3.61	0.03	79%	21%	79%	NaN		Jun	Jun	Mar-Jul	> 200	-
	Gadidae	*Raniceps raninus*	201	1	0.19	-	0%	100%	NaN	NaN		Aug	Aug	Jan-Jun, Oct-Dec	> 100	H
	Phycidae		201	3	1.50	0.01	67%	0%	100%	0%		Mar-Sep	Jun	Mar-Jul	150-300	-
	Lotidae	*Enchelyopus cimbrius*	201	14	5.28	0.11	51%	49%	52%	48%		Jun-Nov	Jun	Jan-Sep	20-250	S, M
	Merlucciidae	*Merluccius merluccius*	201	1	2.77	0.01	0%	100%	NaN	0%		Jul	Jul	Jun-Sep	100-300	-
Perciformes																
	Labridae	*Ctenolabrus rupestris*	201	31	4.34	0.20	47%	13%	68%	89%		Jun-Aug	Jul	Jun-Aug	> 20	Ve
	Labridae	*Labrus* sp.	201	6	8.70	0.13	8%	4%	68%	NaN		Jun-Jul	Jul	Jun-Aug	5-30	H
	Labridae	*Symphodus* sp.	201	7	7.57	0.14	30%	70%	49%	0%		Jun-Aug	Jul	May-Aug	5-30	H
	Ammodytidae	*Ammodytes lancea*	201	56	1.25	0.10	42%	35%	59%	35%		All year	Jul	Mar-May, Oct-Dec	0-30	S
	Callionymidae	*Callionymus* sp.	201	23	5.15	0.15	10%	70%	13%	4%		Jun-Sep	jul	Apr-Sep	> 400	-
	Callionymidae/ Carangidae		201	12	11.15	0.26	6%	70%	15%	0%		Jun-Jul	Jul	Apr-Sep	> 400	-
	Carangidae	*Trachurus trachurus*	201	31	3.65	0.30	24%	60%	13%	82%		Jul-Aug	Jul	May-Oct	> 90	P
	Carangidae		201	26	4.21	0.30	19%	64%	13%	59%		Jul-Aug	Jul	May-Sep	> 90	P
	Gobidae	*Aphia minuta*	201	6	0.46	0.01	25%	75%	NaN	25%		Jul-Aug	Jul	May-Sep	0–10	S, M
	Gobidae	*Crystallogobius nilssonii*	201	6	6.29	0.11	0%	85%	1%	0%		Jul-Aug	Jul	May-Sep	0–10	S, M
	Gobidae	*Pomatoschistus* sp.	201	8	5.74	0.11	4%	96%	5%	0%		Apr-Sep	Jul	May-Sep	0–10	S, M
	Gobidae		201	91	11.63	0.76	33%	41%	41%	38%	20–30	All year	Jul	May-Sep	0–10	S, M
	Pholidae	*Pholis gunellus*	201	1	1.79	0.01	100%	0%	100%	NaN	30	Mar	Mar	Nov-Apr	0-30	Ve
	Scombridae	*Scomber* sp.	201	4	6.06	0.07	12%	88%	16%	0%		Jun-Jul	Jun	May-Sep	> 90	P
	trachinidae	*Trachinus* sp.	201	17	8.71	0.30	62%	38%	61%	58%		Jul-Aug	Jul	Jun-Sep	5-40	S
Pleuronectiformes																
	Bothidae	*Arnoglossus laterna*	201	72	2.55	0.20	37%	61%	40%	34%		Jul-Sep	Jul	Jun-Oct	10-100	-
	Pleuronectidae		201	2	2.58	0.02	0%	31%	0%	NaN		May-Jun	May	Jan-May	10-50	S, M
	Pleuronectidae	*Buglossidium luteum*	201	66	1.28	0.08	18%	74%	10%	28%		Jun-Aug	Jul	Apr-Sep	5-20	S
	Pleuronectidae	*Hippoglossoides platessoides*	201	2	2.12	0.02	68%	32%	68%	NaN		Mar	Mar	Dec-Apr	10-400	M
	Pleuronectidae	*Limanda limanda > 5*	201	17	8.18	0.41	0%	95%	0%	0%		Mar-Jul	Apr	Mar-Jul	> 70	S
	Pleuronectidae	*Limanda limanda ≤ 5*	201	26	33.03	1.54	30%	69%	30%	5%		Mar-Jul	Apr	Mar-Jul	> 70	S
	Pleuronectidae	*Microstomus kitt*	201	2	1.49	0.01	0%	42%	0%	NaN		Jun	Jun	May-Nov	20-150	H
	Pleuronectidae	*Platichtys flesus*	201	12	10.07	0.40	86%	14%	86%	NaN		Jan-Jul	Apr	Jan-Aug	> 25	-
	Pleuronectidae	*Pleuronectes platessa*	201	1	11.23	0.06	0%	100%	NaN	0%		Jul	Jul	Jan-May	10-50	S, M
	Scophthalmidae	*Phrynorhombus norvegicus*	201	1	0.13	-	0%	0%	0%	NaN		Jul	Jul	Apr-Sep		H
	Scophthalmidae	*Psetta/Scophtalmus* sp.	201	4	3.48	0.06	1%	99%	0%	15%		Jun-Aug	Jun	Apr-Sep	20-70	S, M
	Scophthalmidae	*Zeugopterus punctatus*	201	4	1.00	0.01	0%	95%	0%	0%		Jun-Jul	Jun	Mar-Jul		H
	Soleidae	*Solea* sp.	201	5	1.30	0.02	31%	69%	31%	NaN		May-Aug	Jun	Apr-Sep	10-60	S, M
Scorpaeniformes																
	Cottidae	*Myoxocephalus* sp.	201	2	0.80	0.01	37%	63%	0%	100%		Feb-Apr	Apr	Dec-Apr	5-200	Ve
	Cottidae	*Taurulus* sp.	201	2	1.06	0.01	94%	6%	94%	NaN		Apr-Jul	Apr	Feb-Jun	5-200	Ve
	Triglidae		201	1	1.00	-	100%	0%	NaN	100%		Aug	Aug	Apr-Nov	10-150	S, M
	Cyclopteridae	*Cyclopterus lumpus*	201	1	1.83	0.01	0%	100%	NaN	0%		Sep	Sep	Feb-Jun	20-200	H
	Liparidae	*Liparis* sp.	201	2	1.21	0.01	0%	100%	0%	NaN	10-20	Jun	Jun	Jan-May, Sep-Jan	20-50	Ve
	Triglidae	*Eutriglia gurnardus*	201	6	0.87	0.02	0%	86%	0%	0%		Jul-Aug	Jul	Apr-Sep	10-150	S, M
Syngnathiformes																
	Syngnathidae	*Entelurus aequoreus*	201	4	1.38	0.02	87%	3%	0%	100%		Jul-Aug	Aug	Jun-Aug	5-100	Ve
	Syngnathidae	*Nerophis* sp.	201	1	0.19	-	100%	0%	NaN	100%		Aug	Aug	May-Oct	0–15	Ve
	Syngnathidae	*Syngnathus* sp.	201	3	0.20	0.00	63%	0%	100%	100%		Jul	Jul	Jun-Sep	0–15	Ve

Habitat legends denote type of habitat where species are found or an established preference. S=Sand, M=Mud, H=Hard Bottom/substrate, Ve= Vegetation rich bottoms, P=Pelagic, "-" indicates that preference is not known or that information was not found.

Table A1.3. Summary of larval traits and adult distribution of species included in OSPARs list of threatened and/or declining species that are commonly found the Kattegat-Skagerrak region, based on results from plankton surveys and the literature. The table shows the depth distribution, pelagic larval duration (PLD), spawning season, the modeled larval type for each species (see table 5 for details) and adult distribution for a total of 43 species. See appendix B for references.

			Larval traits			Modeled	Adult			
	Family	**Species**	**Depth (m)**	**PLD (d)**	**Season**	**larval type**	**Depth (m)**	**Substrate**	**Distribution**	**References**
Porifera										
Demospongiae	Axinellidae	*Phakellia ventilabrum*	-	< 3 [c]	-	x	35-1900 [a]	H [a]	Skag	6, 31, 41, 15
	Clionaidae	*Cliona celata*	-	< 3 [c]	-	x	3-200 [a]	H [a]	Sw BS- Skag	56, 15
	Mycalidae	*Mycale lingua*	B[c]			x	45-2500 [a]	H [a]	Skag	15
	Geodiidae	*Geodia baretti*	-	< 3 [c]	-	x	40-300 [a]	S,H [a]	Skag	50, 15
Cnidaria						x				
Anthozoa	Pleuxauridae	*Paramuricea placomus*	-	< 1 [b]	Summer [b]	x	83-110 [a]	H [a]		43, 60
		Swiftia rosea	-	< 1 [b]	-	x	18-400 [a]	H [a]	Katt-Skag	60, 15
		Swiftia pallida	-	< 1 [b]	-	x	< 50 [b]	H [b]		60
	Clavulariidae	*Sarcodictyon roseum*	-	< 1 [c]	-	x	20-850 [a]	S,H [a]	Katt-Skag	39, 15
	Actiniidae	*Urticina eques*	-	11-30 [b]	Apr-Jun [b]	C2	< 100 [b]	H [b]		36, 60
	Actinostolidae	*Actinostola callosa*	-	11-30 [c]	Jun-Aug [b]	C2	40-220 [a]	H [a]	Katt-Skag	44, 15
	Caryophylliidae	*Caryophyllia smithii*	-	56-70 [a]	Jan-Mar [a]	C2	10-200 [a]	H [a]	Katt-Skag	56, 35, 57, 4, 15
		Lophelia pertusa	-	~ 35 [a]	Jan-Feb [a]	C2	82-480 [a]	H [a]	Skag	61, 23, 18, 15
	Funiculinidae	*Funiculina quadrangularis*	-	2-10 [c]	Oct-Jan [a]	C1	25-2500 [a]	M [a]	Skag	11, 35, 15
	Virgulariidae	*Virgularia mirabilis*	-	2-10 [a]	Oct-Jan [a]	C1	10-360 [a]	S, M [a]	Katt-Skag	7, 35, 15
		Virgularia tuberculata	-	2-10 [b]	Oct-Jan [a]	C1	10-400 [b]	S, M [b]	Katt-Skag	7, 35, 15
		Stylatula elegans	-	2-10 [b]	Oct-Jan [a]	C1	10-400 [b]	S, M [b]		7, 35
	Kophobelemnidae	*Kophobelemnon stelliferum*	-	2-10 [c]	Oct-Jan [a]	C1	40-1500 [a]	S, M [a]	Skag	45, 7, 35 , 15
Hydrozoa	Plumulariidae	*Nemertesia spp*	-	< 1	Oct-Jan [a]	x	19-225 [a]	S,H [a]	Skag	20, 8, 15
Annelida										
Polychaeta	Sabellidae	*Sabella pavonina*	0-50 [c]*	< 21 [b]	Oct-Jan [a]	C3	5-750 [a]	M,S,H [a]	Katt-Skag	14, 54, 37, 30, 15
Mollusca										
Bivalvia	Mytilidae	*Mytilus edulis*	0-50 [c]*	30-180 [a]	Apr-Sep [a]	B3	0-10 [a]	H,M [a]	Sw BS- Skag	2, 3, 53, 49, 15
		Modiolus modiolu	0-50 [c]*	11-30 [e]	Apr-Jul [a]	B3	1-50 [a]	S,H [a]	Katt-Skag	12, 60, 15
	Limidae	*Acesta excavata*	0-50 [c]*	30-180 [d]	-	C4	50-300 [a]	H [a]	Skag	22, 15
	Arcticidae	*Arctica islandica*	0-50 [c]*	30-60 [a]	Jun-Aug [a]	C4	2-200 [a]	S,M [a]	Skag	33, 28, 53, 58, 34, 15
	Ostreoidae	*Ostrea edulis*	0-50 [c]*	11-30 [a]	Jun-Sep [a]	B3	0-10 [a]	S,M [a]	Katt-Skag	60, 15
Crustacea										
Decapoda	Pandalidae	*Dichelopandalus bonnieri*	0-30 [b]*	30-180 [b]	Nov-Jan [a]	C4	30-400 [a]	G, S, M [a]		17,51, 60
	Thiidae	*Thia scutellata*	20-30 [a]*	30-60 [c]	Jan-Mar [a]*	C4	>30 [a]	S [a]	Katt-Skag	42, 15
	Atelecyclidae	*Atelecyclus rotundatus*	0-30 [a]*	40-46 [a]	Jan-Feb [a]*	C4	12-300 [a]	S, G [a]	Katt-Skag	17, 19, 24, 15
	Corystidae	*Corystes cassivelaunus*	0-50 [a]*	11-30 [a]	Mar-Aug [a]*	C3	7-90 [a]	S, M, G [a]	Katt-Skag	17, 60, 15
	Axiidae	*Calocaris macandreae*	0-30 [b]*	30-60 [c]	Jan-Aug [b]*	C5	12-1070 [a]	M [a]	Katt-Skag	21, 15
		Calocarides coronatus	0-30 [b]*	30-60 [c]	Jan-Aug [b]*	C5	80-1200 [a]	M [a]	Skag	29, 15
	Callanassidae	*Callianassa subterranea*	0-30 [b]*	30-60 [a]	Jul-Sep [b]*	C4	30-60 [a]	M, S [a]	Skag	48, 59, 17, 15
	Ampeliscidae	*Haploops tubicola*	B[c]	-	Jan-Mar [b]	x	20-200 [a]	M, S [b]	Katt-Skag	46, 15
		Haploops tenuis	B[c]	-	Jan-Mar [b]	x	20-200 [b]	M, S [b]	Katt-Skag	46, 15
Bryozoa										
Gymnolaemata	Phidoloporidae	*Reteporella beaniana*	0-50 [d]*	< 1 [d]	Oct-Jan [a]	x	10-1006 [a]	H [a]	Katt-Skag	9, 60 , 15
Echinodermata										
Asteroidae	Stichasteridae	*Stichastrella rosea*	0-50 c*	90-180 [c]	Oct-Jan [a]	C5	18-200 [a]	G, S, H [a]	Katt-Skag	18, 15
Crinoidea	Antedonidea	*Antedon petasus*	0-50 d*	2-10 [b]	Oct-Jan [a]	C1	20-326 [a]	S,H [a]	Katt-Skag	38, 32, 60, 15
		Hathrometra sarsii	0-50 d*	2-10 [b]	Oct-Jan [a]	C1	28-1783 [a]	H [a]	Katt-Skag	38, 32, 60, 15
Ophiuridea	Gorgonocephalidae	*Gorgonocephalus caputmedusae*	0-50 c*	-	Oct-Jan [a]	C3	50-200 [a]	H [a]	Skag	47, 15
Chordata										
Leptocardii	Branchiostomatidae	*Branchiostoma lanceolatum*	-	~ 4 [e]	-	x	5- > 30 [a]	S, M [a]	Skag	10, 60, 15
Ochrophyta										
Phaeophyceae	Laminariaceae	*Saccharina latissima*	-	2-4 [e]	Oct-Jan [a]	x	< 30 [a]	H, G [a]		5, 40, 26
		Laminaria hyperborea	-	1 [a]	Oct-Jan [a]	x	< 30 [a]	H, G [a]		13, 25, 26
Tracheophyta										
Magnoliidae	Zosteraceae	*Zostera marina*	0 [a]*	7-14 [a]	Jun-Sep[a]	A1	0-12 [a]			1, 16, 27
		Zostera noltii	0 [b]*	7-14 [b]	Jun-Sep[a]	A1	0-12 [b]			16, 27

Letters denote B = Benthic larva, * = data from this study, - = no information available, a-d = resolution used to describe the larval traits (a = species, b = Family, c= Order/Class, d=Phyla)

For modeled larval types letters denote the 14 larval types described in table . x = not included in model due to benthic larval stage or pelagic larval stage < 5 d.

Habitat letters denote: M=mud, S=Sand, G=gravel, H=hard substrate

Skag = Skagerrak, Katt = Kattegat, Sw BS = southwest Baltic Sea

Table A1.4. Summary of 31 OSPAR-MPAs that are located within the study area (Kattegat and Skagerrak), at 0-100 m depth, larger than 1 km2 and that includes protection of benthic habitats, which were included in OSPAR-MPA network in the model study. Map ID refers to the location of the MPA on the map in Fig. 5. N2000 = Natura 2000 MPA, NR = Nature Reserve, DEN = Denmark, SWE = Sweden and NOR = Norway.

Map ID	MPA name	MPA type	OSPAR ID	Country	Area (km^2)
21	Anholt og havet nord for	OSPAR, N2000		DEN	482.0
29	Ebbeløkke Rev	OSPAR, N2000	O-DK-00VA330	DEN	1.4
16	Fladen	OSPAR, N2000	O-S-0510127	SWE	103.9
27	Gilleleje Flak og Tragten	OSPAR, N2000	O-DK-00VA171	DEN	151.2
1	Gule Rev	OSPAR, N2000	O-DK-00VA259	DEN	475.3
7	Gullmarsfjorden	OSPAR, NR, N2000	O-S-0520171	SWE	114.0
28	Havet og kysten mellem Hundested og Rørvig	OSPAR, N2000	O-DK-005Y220	DEN	40.4
13	Havet omkring Nordre Rønner	OSPAR, N2000	O-DK-00FX257	DEN	186.7
8	Havstensfjorden-Svälte kile	OSPAR, NR, N2000	O-S-0520173	SWE	12.6
11	Herthas Flak	OSPAR, N2000	O-DK-00VA248	DEN	13.9
26	Hesselø med omliggende stenrev	OSPAR, N2000	O-DK-003X202	DEN	42.2
12	Hirsholmene, havet vest herfor og Ellinge Ås udløb	OSPAR, N2000	O-DK-00FX113	DEN	95.3
17	Kims Top og den Kinesiske Mur	OSPAR, N2000	O-DK-00VA247	DEN	262.6
4	Knudegrund	OSPAR, N2000	O-DK-00VA302	DEN	7.5
30	Kobberhage kystarealer	OSPAR, N2000	O-DK-00DX322	DEN	8.0
6	Kosterfjorden-Väderfjorden	OSPAR, NP, NR, N2000	O-S-0520170	SWE	535.6
10	Kungsbackafjorden	OSPAR, NR, N2000	O-S-0510058	SWE	78.7
14	Læsø Trindel og Tønneberg Banke	OSPAR, N2000	O-DK-00VA249	DEN	86.8
18	Lilla Middelgrund	OSPAR, N2000	O-S-0510126	SWE	178.6
3	Lønstrup Rødgrund	OSPAR, N2000	O-DK-00VA301	DEN	93.6
25	Lysegrund	OSPAR, N2000	O-DK-00VA299	DEN	31.8
20	Morups bank	OSPAR, N2000	O-S-0510187	SWE	5.7
9	Nordre älvs estuarium	OSPAR, NR, N2000	O-S-0520043	SWE	70.9
24	Schultz og Hastens Grund samt Briseis Flak	OSPAR, N2000	O-DK-00VA303	DEN	208.9
31	Skagen Gren	OSPAR, N2000		DEN	2711.0
22	Stora Middelgrund och Röde bank	OSPAR, N2000	O-S-0510186	SWE	114.2
23	Store Middelgrund	OSPAR, N2000	O-DK-00VA250	DEN	21.5
2	Store Rev	OSPAR, N2000	O-DK-00VA258	DEN	109.9
15	Strandenge på Læsø og havet syd herfor	OSPAR, N2000	O-DK-00FX010	DEN	1041.7
5	Ytre Hvaler	OSPAR, NP	O-N-010	NOR	355.3
19	Ålborg Bugt, Randers Fjord og Mariager Fjord	OSPAR, N2000	O-DK-00FX122	DEN	716.4

Table A1.5. Summary of other MPAs (than OSPAR-MPAs) that were included in the model study. All MPAs are located at 0-100 m depth within the study area (Kattegat and Skagerrak) or in the Danish Belt or the Öresund Straight. They are all lager than 1 km2 and include protection of benthic habitats. Map ID refers to the location of the MPA on the map in Fig. 5. Letters or numbers with parenthesis indicate that they are located close to the indicated MPA in Fig. 5. DEN = Denmark, SWE = Sweden and NOR = Norway.

Map ID	MPA name	MPA type	Country	Area (km2)
x	Begtrup Vig og kystområder ved Helgenæs	Natura 2000	DEN	17.8
g	Breviks kile-Toftenäs	Natura 2000	SWE	7.8
(a)	Buvika/Rødskjær	Nature Reserve	NOR	1.8
ø	Centrale Storebælt og Vresen	Natura 2000	DEN	376.1
j	Ersdalen	Nature Reserve	SWE	5.3
t	Falsterbohalvön	Natura 2000	SWE	
ä	Fyns Hoved, Lillegrund og Lillestrand	Natura 2000	DEN	22.0
(20)	Gamla Köpstad	Natura 2000	SWE	3.2
(a)	Grunnane	Nature Reserve	NOR	2.9
(8)	Gustavsbergsområdet	Nature Reserve	SWE	2.8
n	Hallands Väderö	Natura 2000	SWE	18.4
(7)	Hållöarkipelagen	Nature Reserve	SWE	2.9
(e)	Halsefjorden	Natura 2000	SWE	12.1
d	Härmanö	Natura 2000	SWE	14.9
g	Härön	Natura 2000	SWE	7.1
w	Hatter Barn	Natura 2000	DEN	6.4
ä	Havet mellem Romsø og Hindsholm samt Romsø	Natura 2000	DEN	43.6
y	Horsens Fjord, havet øst for og Endelave	Natura 2000	DEN	461.6
(5)	Idefjorden	Natura 2000	SWE	8.8
(m)	Jonstorp-Vegeåns mynning	Natura 2000	SWE	12.8
(b)	Jorefjorden	Natura 2000	SWE	6.3
(x)	Kaløskovene og Kaløvig	Natura 2000	DEN	7.5
	Kalvön	Nature Reserve	SWE	1.3
h	Klåverön	Nature Reserve	SWE	
(e)	Koljön	Nature Reserve	SWE	1.2
(e)	Koljön	Nature Reserve	SWE	1.2
(b)	Koster	Natura 2000	SWE	11.7
	Kråkerøy-skjærgården	Nature Reserve		4.3
o	Kullaberg-Skälderviken	Natura 2000	SWE	13.6
(a)	Kultane/Skarvesete	Nature Reserve	NOR	1.3
(a)	Kurefjorden	Nature Reserve	NOR	3.9
(28)	Kyndby Kyst	Natura 2000	DEN	3.6
p	Knähaken	Nature Reserve	SWE	
(8)	Lilla Hasselön	Nature Reserve	SWE	2.2
ö	Lillebælt	Natura 2000	DEN	353.3
(q)	Lommabukten	Natura 2000	SWE	2.2
q	Lundåkrabukten	Natura 2000	SWE	
(7)	Malmöfjord	Natura 2000	SWE	7.0
d	Måseskär	Natura 2000	SWE	18.0
x	Mejl Flak	Natura 2000	DEN	39.3
(e)	Morlanda	Nature Reserve	SWE	7.9
(20)	Morups tånge	Natura 2000	SWE	2.1
w	Munkegrunde	Natura 2000	DEN	13.4
(c)	Näverkärr	Natura 2000	SWE	2.3
l	Nidingen	Natura 2000	SWE	7.3
(i)	Nordön	Nature Reserve	SWE	4.3
ä	Odense Fjord	Natura 2000	DEN	50.8
h	Pater Noster-skärgården	Natura 2000	SWE	24.2
(v)	Roskilde Fjord	Natura 2000	DEN	149.0
z	Røsnæs, Røsnæs Rev og Kalundborg Fjord	Natura 2000	DEN	57.0
(29)	Ryggen	Natura 2000	DEN	4.4
(h)	Sälöfjorden	Natura 2000	SWE	28.7
r	Saltholm og omliggende hav	Natura 2000	SWE	72.6
(c)	Sandön	Nature Reserve	SWE	1.3
(b)	Sannäsfjorden	Natura 2000	SWE	4.4
q	Saxåns mynning-Järavallen	Natura 2000	SWE	19.6
v	Sejerø Bugt og Saltbæk Vig	Natura 2000	DEN	446.5
(c)	Soteskär	Natura 2000	SWE	3.0
w	Stavns Fjord, Samsø Østerflak og Nordby Hede	Natura 2000	DEN	157.7
f	Stenungsundskusten	Natura 2000	SWE	21.5
u	Stevns Rev	Natura 2000	DEN	46.7
e	Stigfjorden	Natura 2000	SWE	48.4
(7)	Strömmarna	Natura 2000	SWE	4.5
(e)	Sundsby	Natura 2000	SWE	3.6
b	Tanumskusten	Natura 2000	SWE	82.8
(h)	Tofta	Nature Reserve	SWE	6.3
(b)	Trossö-Kalvö-Lindö	Natura 2000	SWE	8.9
(b)	Ulön-Dannemark	Nature Reserve	SWE	3.1
(e)	Valön	Nature Reserve	SWE	2.7
(j)	Vargö	Nature Reserve	SWE	1.4
(18)	Västra Getterön	Natura 2000	SWE	1.8
m	Vendelsöarna	Nature Reserve	SWE	
s	Vestamager og havet syd for	Natura 2000	DEN	62.1
j	Vinga	Nature Reserve	SWE	5.6
k	Vrångöskärgården	Natura 2000	SWE	70.1
c	Åbyfjorden	Natura 2000	SWE	11.0
å	Æbelø, havet syd for og Nærå	Natura 2000	DEN	132.6
i	Älgön-Brattön	Natura 2000	SWE	11.9
(i)	Ödsmåls Kile	Natura 2000	SWE	2.4
a	Øra	Nature Reserve	NOR	16.8

Table A1.6. Summary of 14 larval types assessed in the model study, and examples of species that are represented by the different larval traits.

Larval types	Code	Depth (m)	PLD (d)	Ex. of taxa
Simple larval types	**A1**	100% 0-2 m	10 d	
	A2	100% 24-26 m	10 d	
	A3	100% 0-2 m	30 d	
	A4	100% 24-26 m	30 d	
Shallow habitats (1-20 m)	**B1**	80% 0-2 m 20% 10-12m 0% 24-26 m 0% 48-50 m	50% 5 d 50% 10d	Algal spores
	B2	80% 0-2 m 20% 10-12m 0% 24-26 m 0% 48-50 m	50% 20 d 50% 30 d	*Asterias* sp., pipefish-juveniles
	B3	10% 0-2 m 40% 10-12m 40% 24-26 m 10% 48-50 m	50% 20 d 50% 30 d	Balanidae, *Mytilus edulis*, *Ostrea edulis, Littorina littorea*
	B4	30% 0-2 m 10% 10-12 m 50% 24-26 m 10% 48-50 m	70% 30 d 30% 60 d	*Carcinus maenas, Palaemon sp., Crangon crangon,* Labridae, Gobidae
	B5	20% 0-2 m 50% 10-12m 20% 24-26 m 10% 48-50 m	100% 60 d	*Gadus morhua*
Deep habitats (21-100 m)	**C1**	0% 0-2 m 20% 10-12 m 40% 24-26 m 40% 48-50 m	100% 10d	Anthozoa, Crinoidea
	C2	0% 0-2 m 20% 10-12m 40% 24-26 m 40% 48-50 m	100% 30 d	Ophiurida, *Luidia sarsi* Paguridae, Pisidia sp. *Limanda limanda*
	C3	10% 0-2 m 40% 10-12m 40% 24-26 m 10% 48-50 m	100% 30 d	Echinoida, Spionida, *Sabella* sp. *Nephrops norvegicus* *Corystes cassivelanuas*
	C4	10% 0-2 m 40% 10-12m 40% 24-26 m 10% 48-50 m	100% 60 d	*Artica islandica, Cancer pagurus,* Gadidae spp.
	C5	40% 0-2 m 30% 10-12m 20% 24-26 m 10% 48-50 m	100% 30 d	*Calocaris macandrea.* *Liocarcinus navigator,* *Platichtys flesus*

APPENDIX B

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Additional references

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Per Jonson, Department of Biology and Environmental Sciences, University of Gothenburg, Sweden, unpublished data

APPENDIX C

GRAPHS OF THE DEPTH DISTRIBUTION AND SPAWNING SEASON OF INVERTEBRATE AND FISH LARVAE COLLECTED IN SKAGERRAK AND KATTEGAT

Photos: Erik Selander

Description of the data

The data presented in the graphs was collected using an opening and closing circular plankton net (250 µm mesh, 0.5 m^2 opening) that sampled at fixed depths from the surface down to 40 m (referred to as "single net" in the graphs), or using a multinet plankton sampler (Hydro-bios) with a 0.5x0.5 m opening fitted with 5 separate nets equipped with 300 µm mesh that fished at discrete 10 to 20 m intervals from 50 m up to the surface (referred to as "multinet" in the graphs). The single net samples were mainly collected during the summer month 2005–2007 whereas the multinet samples were collected monthly during a 13 month period 2009-2010. In total 330 plankton samples were analysed, but not all larval species and stages were analysed in all samples and the number of replicates per taxa and stage varies between 132 and 330.

Explanation of the appendix and graphs

A total of 80 taxa and stages of invertebrate larvae and 45 taxa of fish larvae were identified in the study, and their depth distribution and seasonal occurrence are graphically presented in the appendix. The results for each larval taxa are shown on two separate pages (referred to as plates). First the depth distribution is shown for all invertebrate larvae followed by the seasonal pattern for the same taxa. Thereafter the same types of graphs are shown for the fish taxa (plate 134–220).

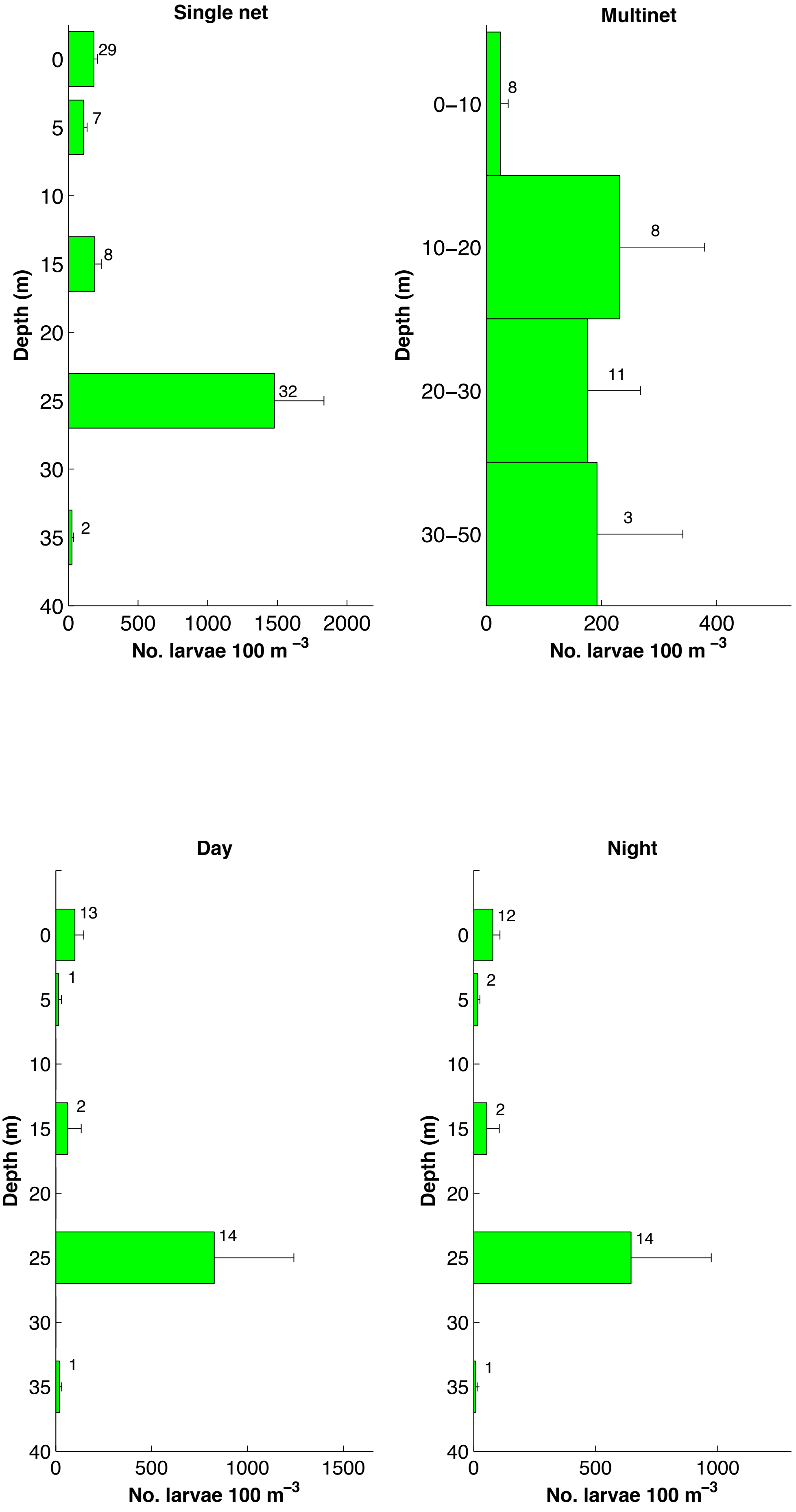
The plates showing the depth distribution contains up to 4 graphs per taxa: 3 graphs from the single net samples (based on all samples, only day or only night samples) and one graph from the multinet samples (all samples). Each graph shows the average abundance (100 m^{-3}; +SE) based on all samples in which the taxa was analyzed. The number presented by each bar denotes the number of samples in which the taxa occurred (N) at the specified depth. Please note that the scale of the x-axis varies between graphs. In the graphs showing the seasonal pattern of abundance, the average abundance (100 m^{-3}; +SE) per month is estimated based on all single and multinet samples.

TABLE OF CONTENTS – NUMERICAL ORDER

TABLE OF CONTENTS – ALPHABETICAL ORDER

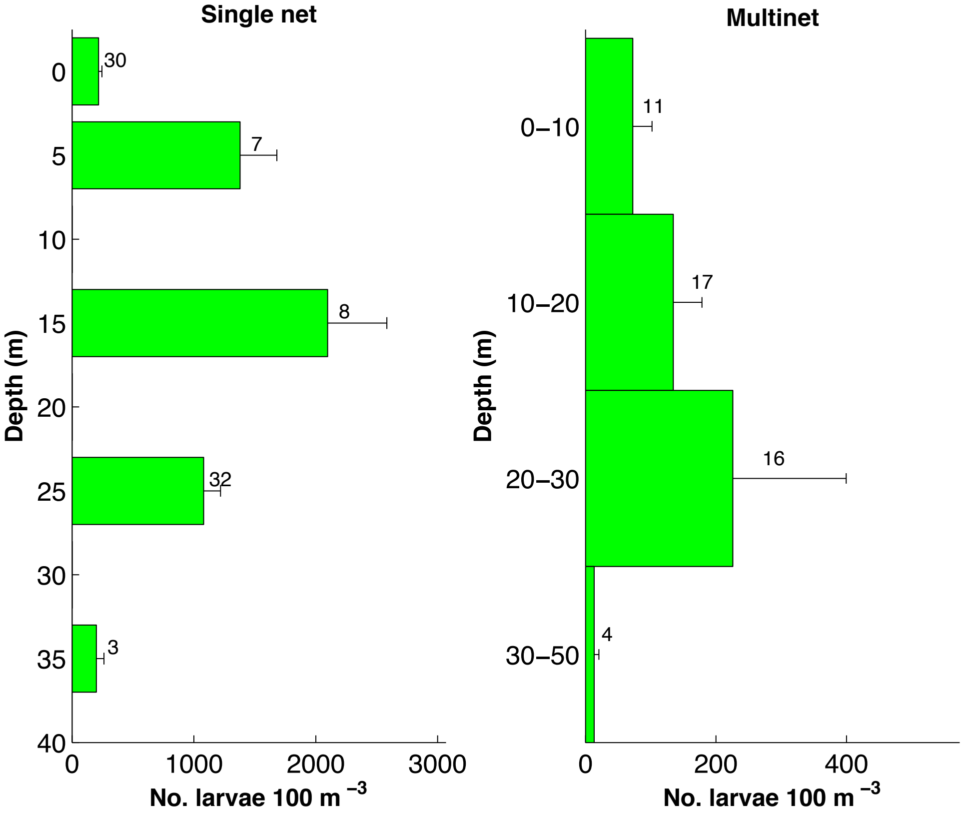
1

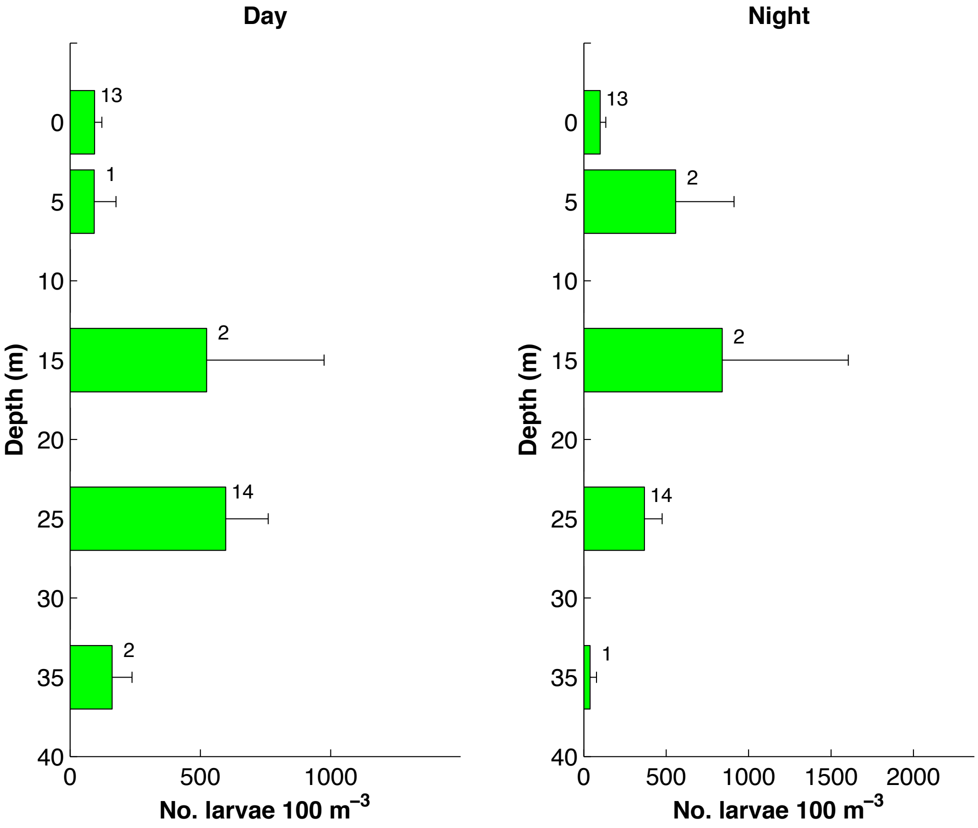
Bivalve veliger larva



2

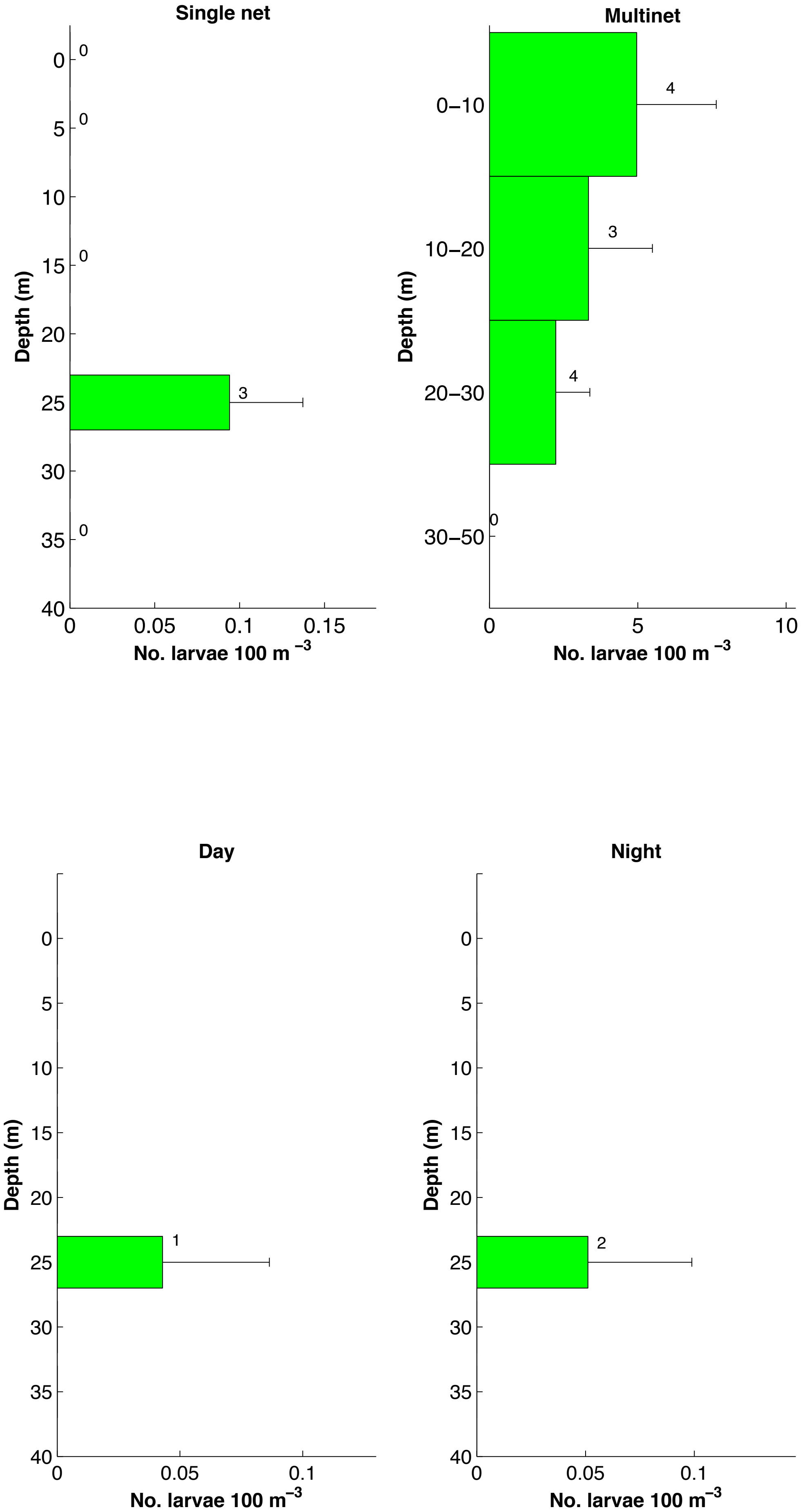
Gastropod veliger larva





3

Nudibranchia (cf.)



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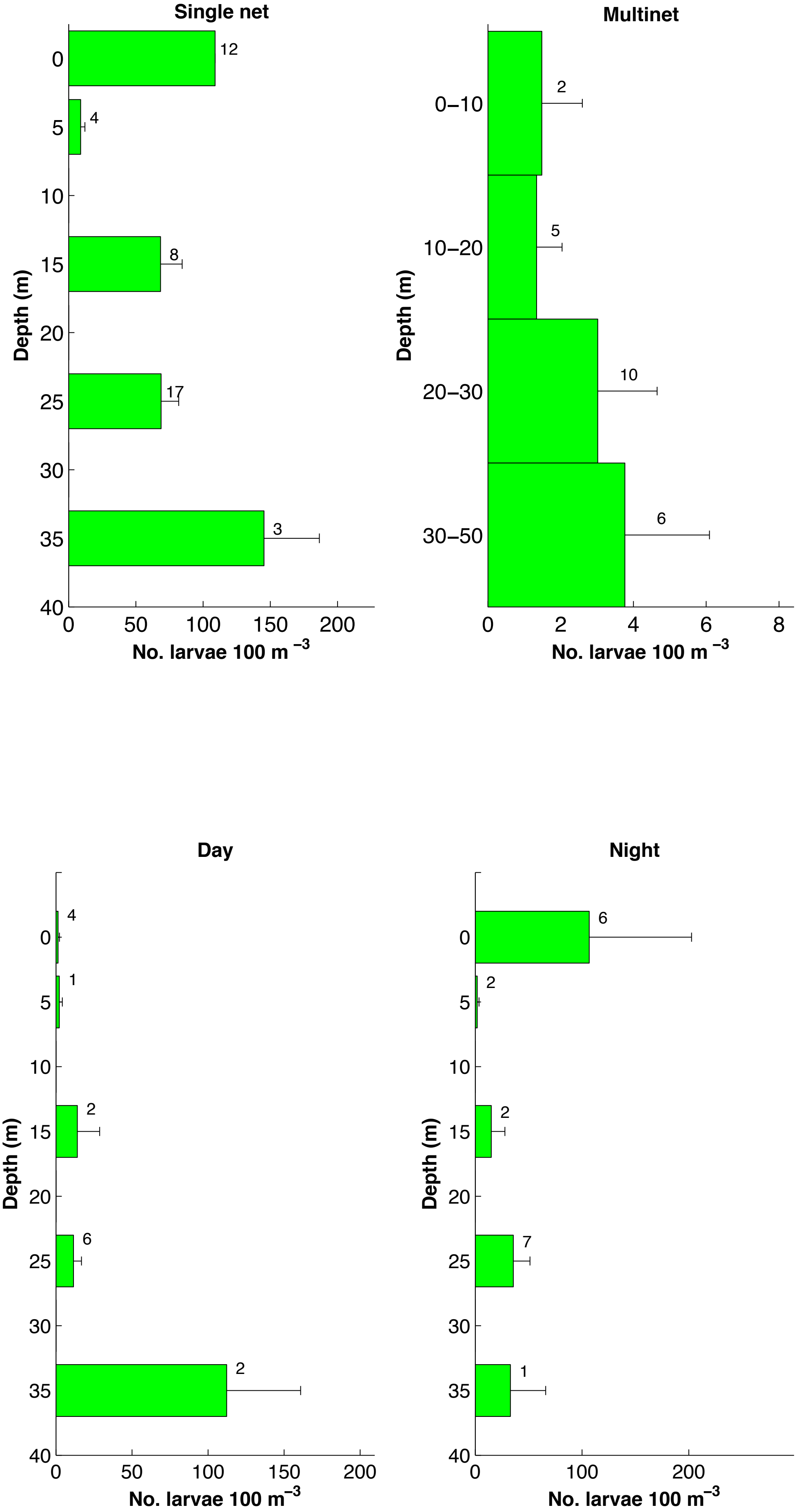
Trocophore larva



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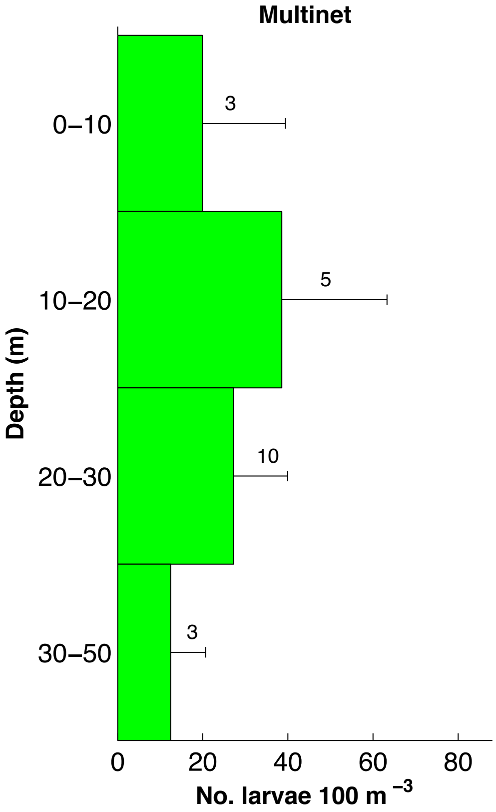
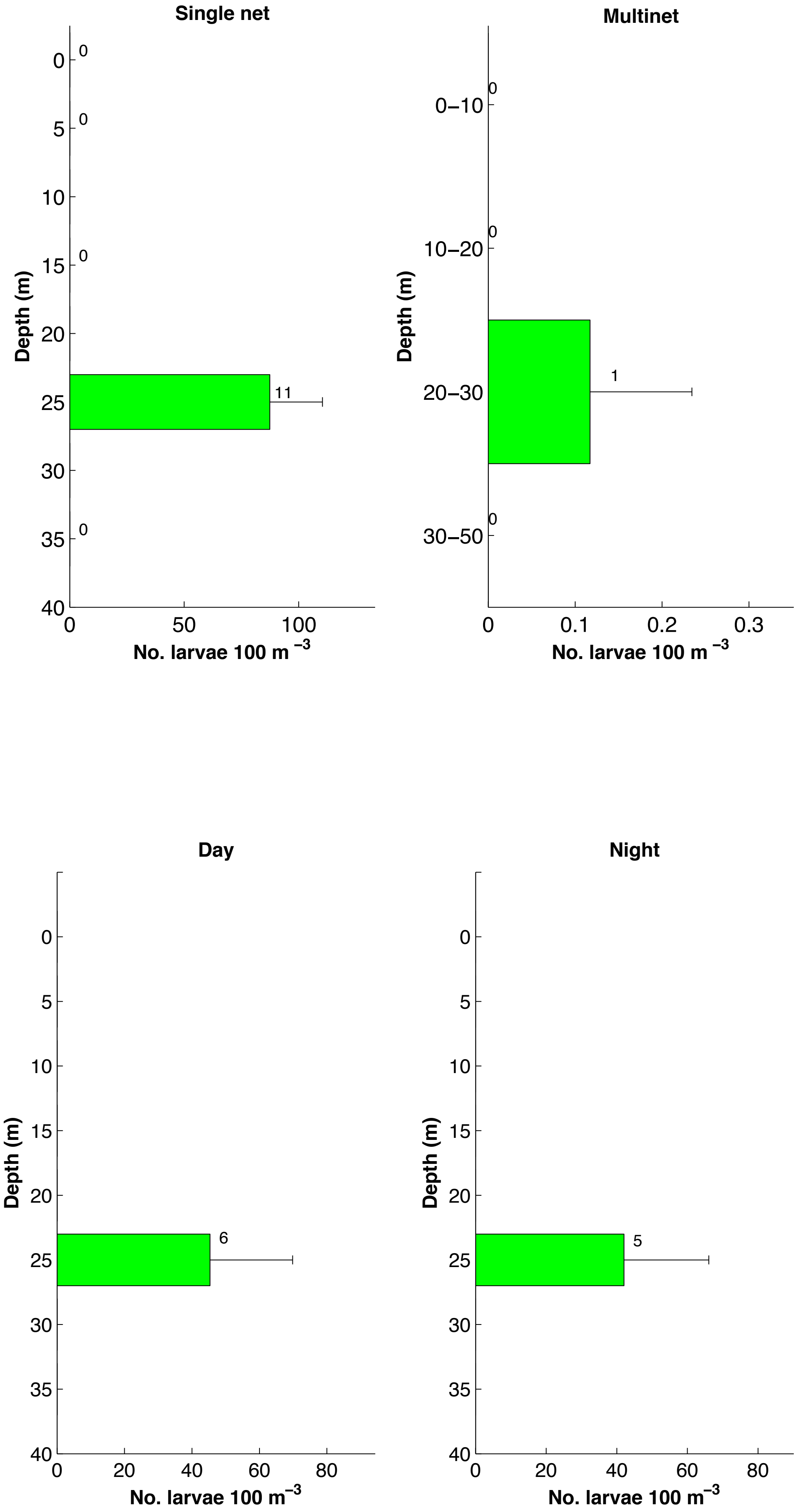
Spionid sp.


Multinet
Depth (m)
0–10
10–20
20–30
30–50
3
5
10
3
0
20
40
60
80
No. larvae 100 m $^{-3}$

6

Poecilochaetidae



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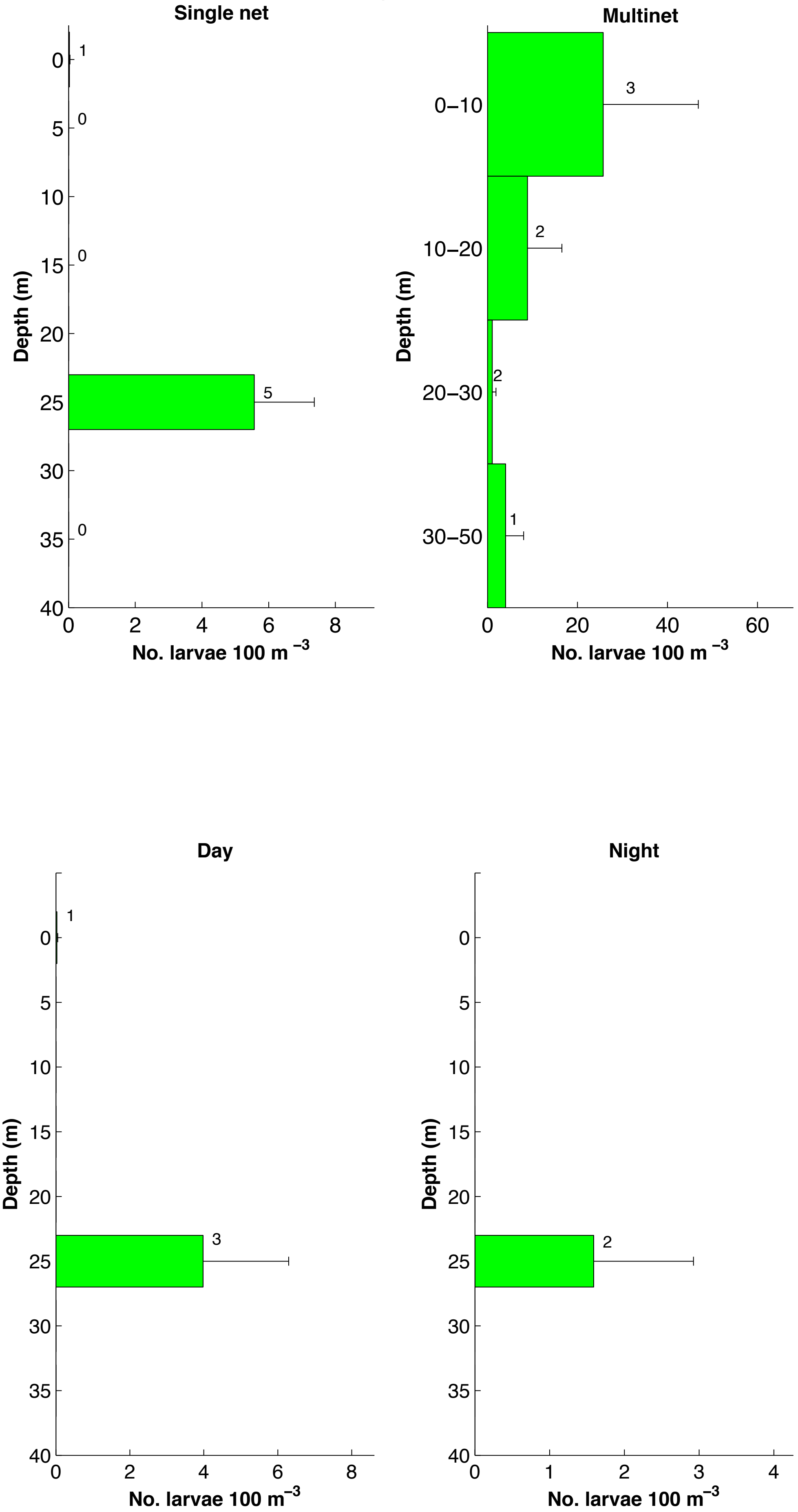
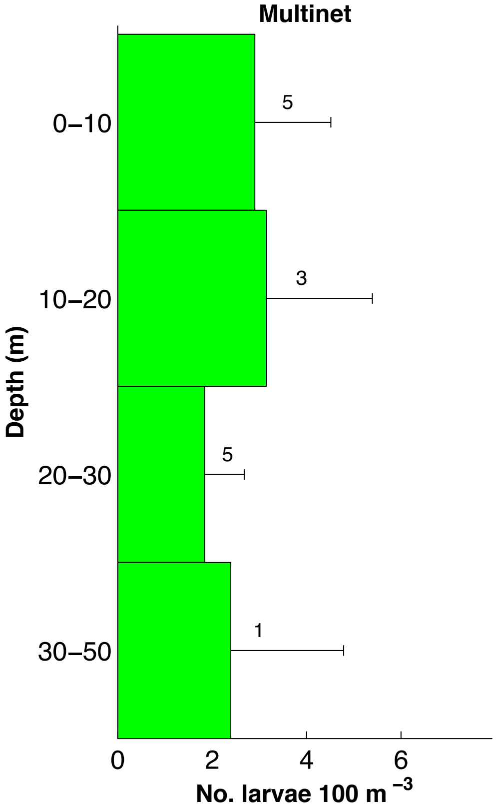
Polynoidae



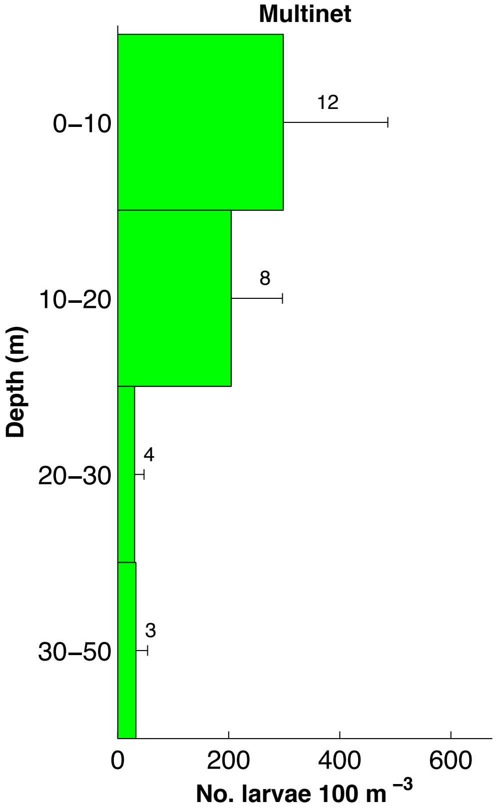
8

Phoronid larva



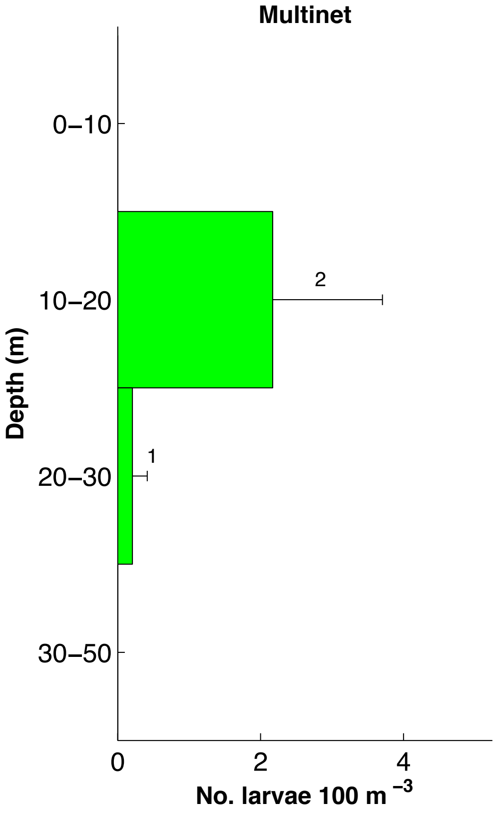
9

Cyphonautes larva



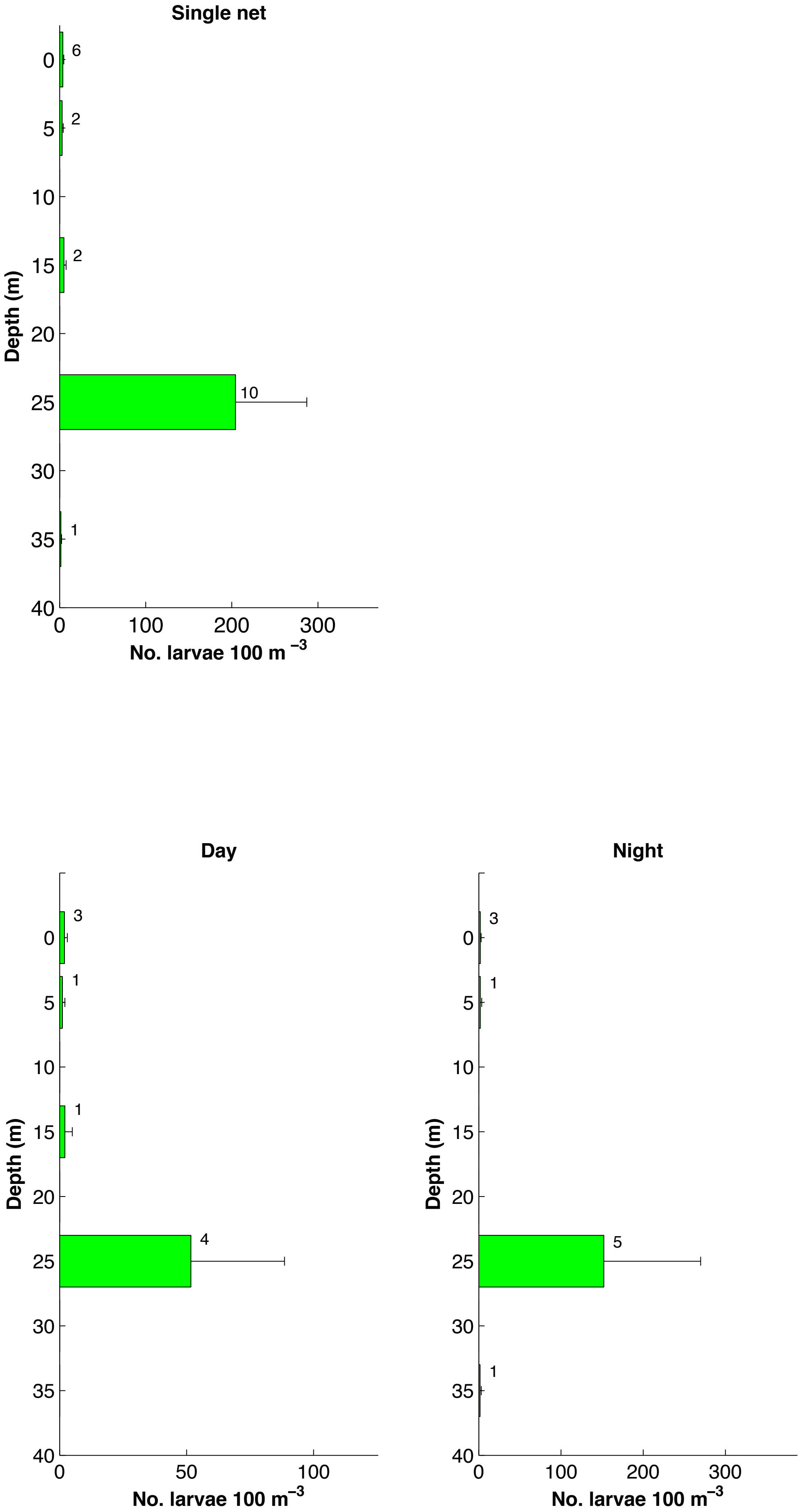
10

Cnidaria



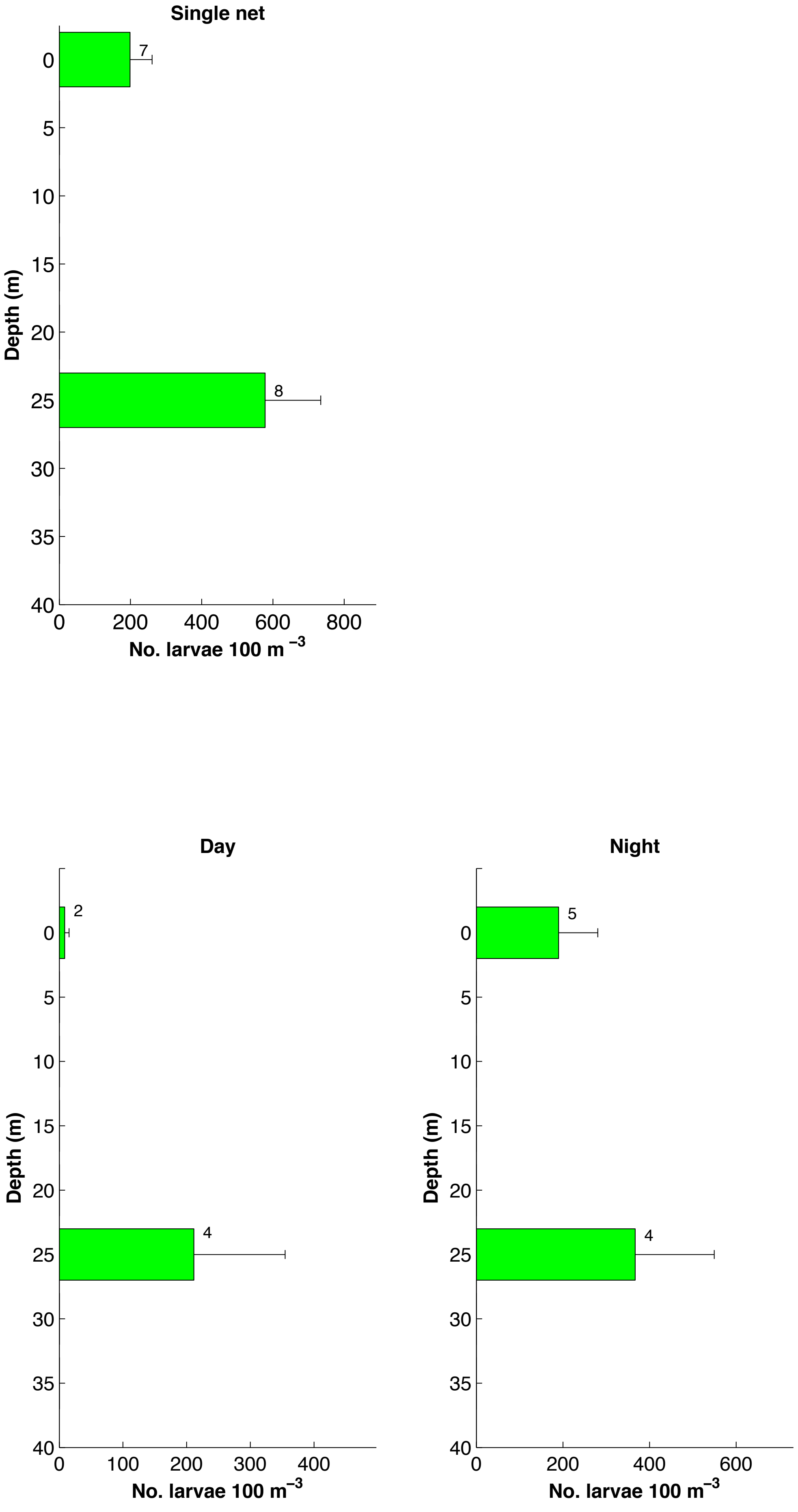
11

Echinodermata spp.



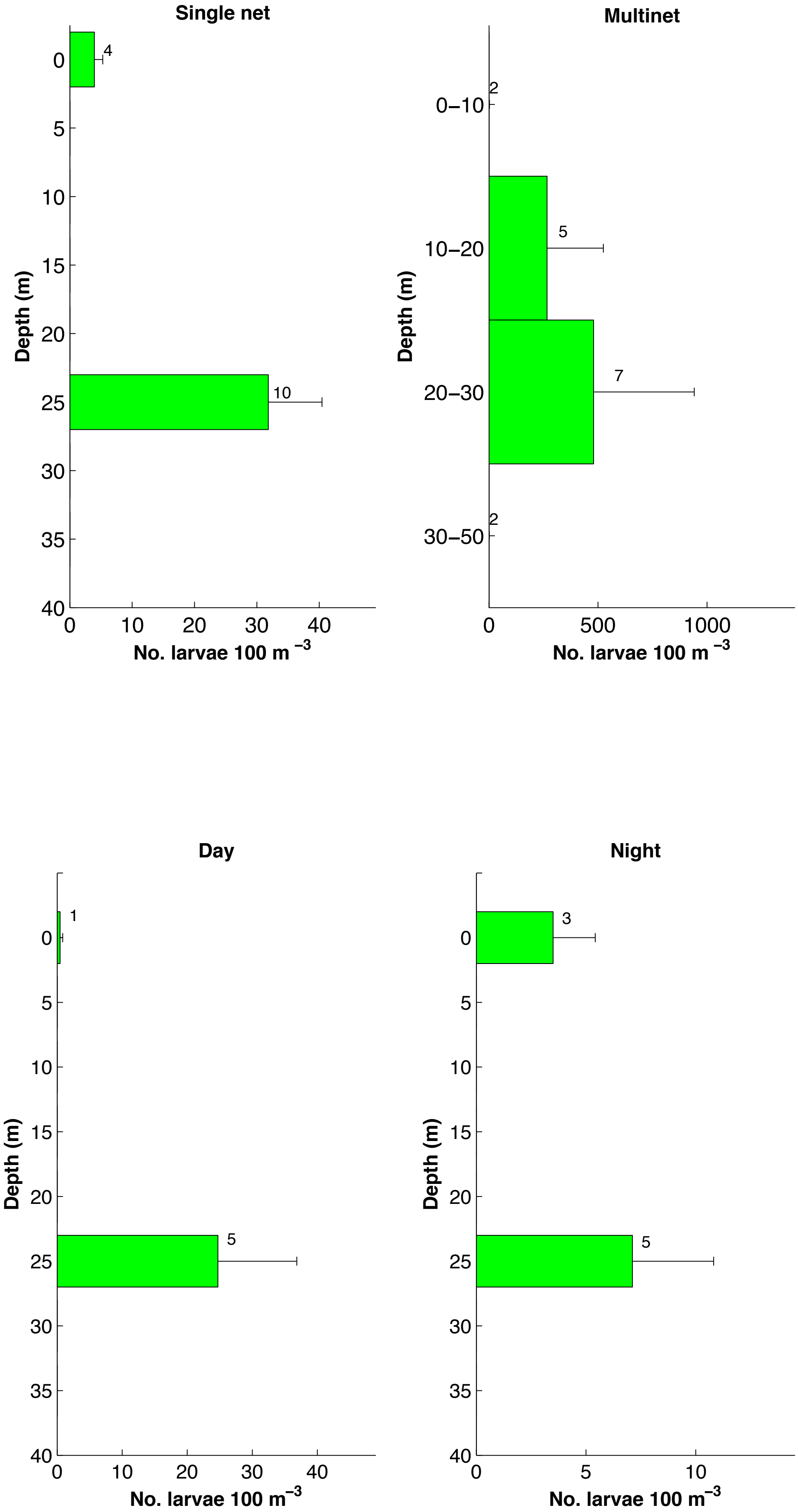
12

Pluteus larva



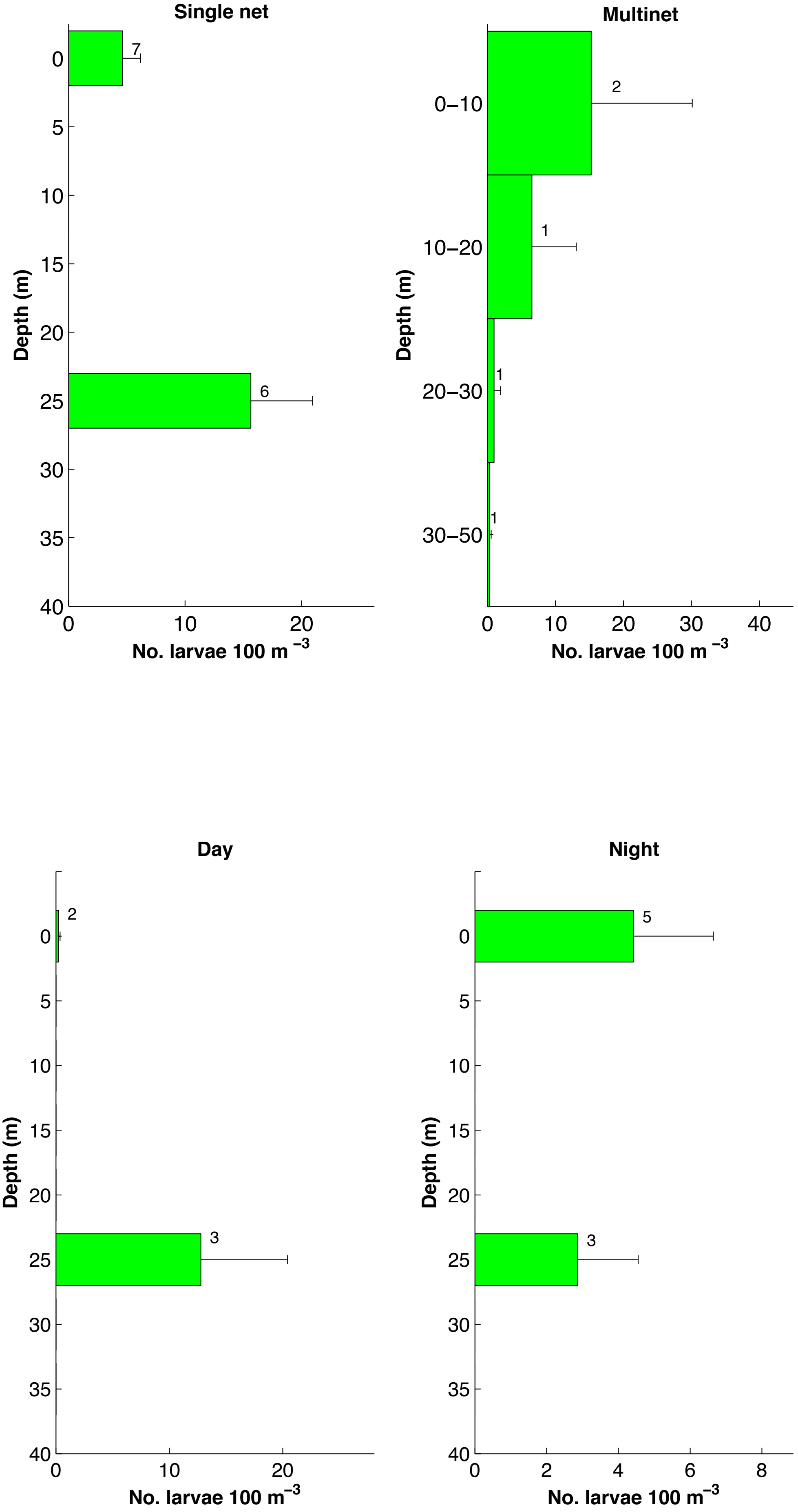
13

Ophiurid juvenile

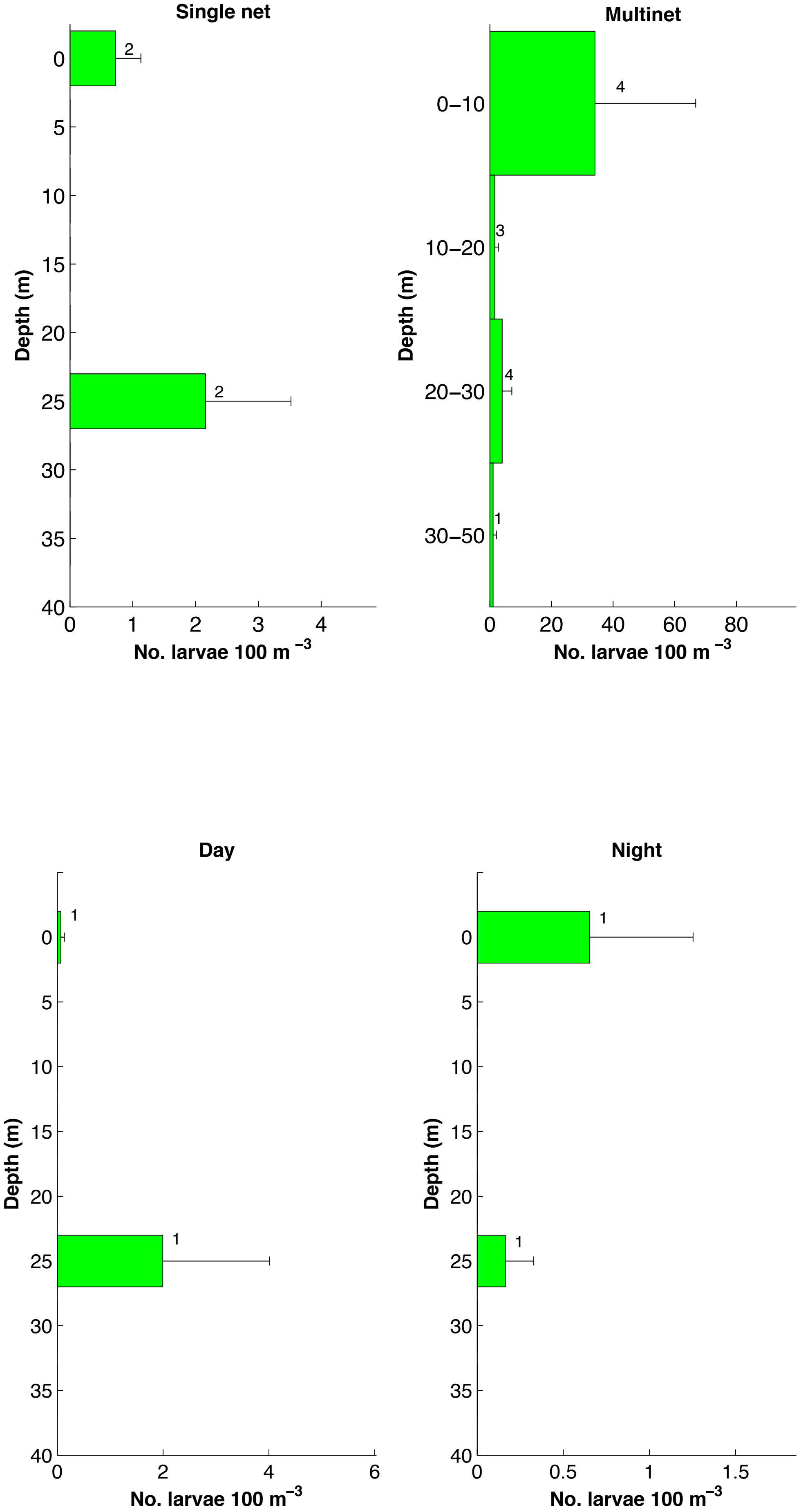


14

Echinoid juvenile

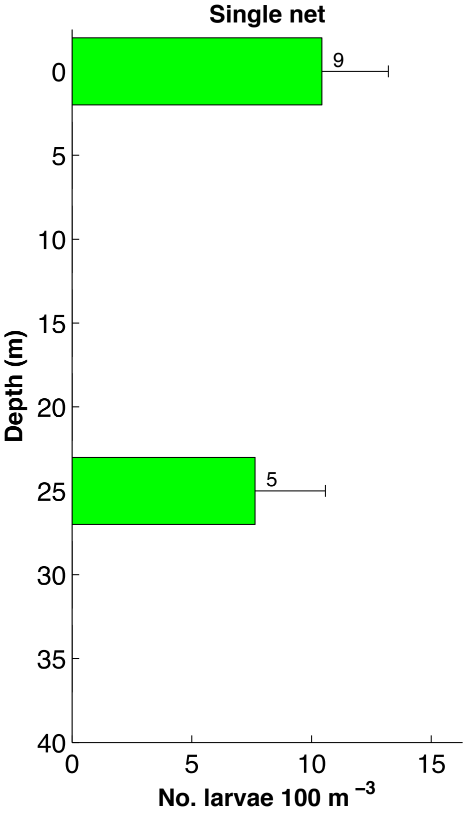


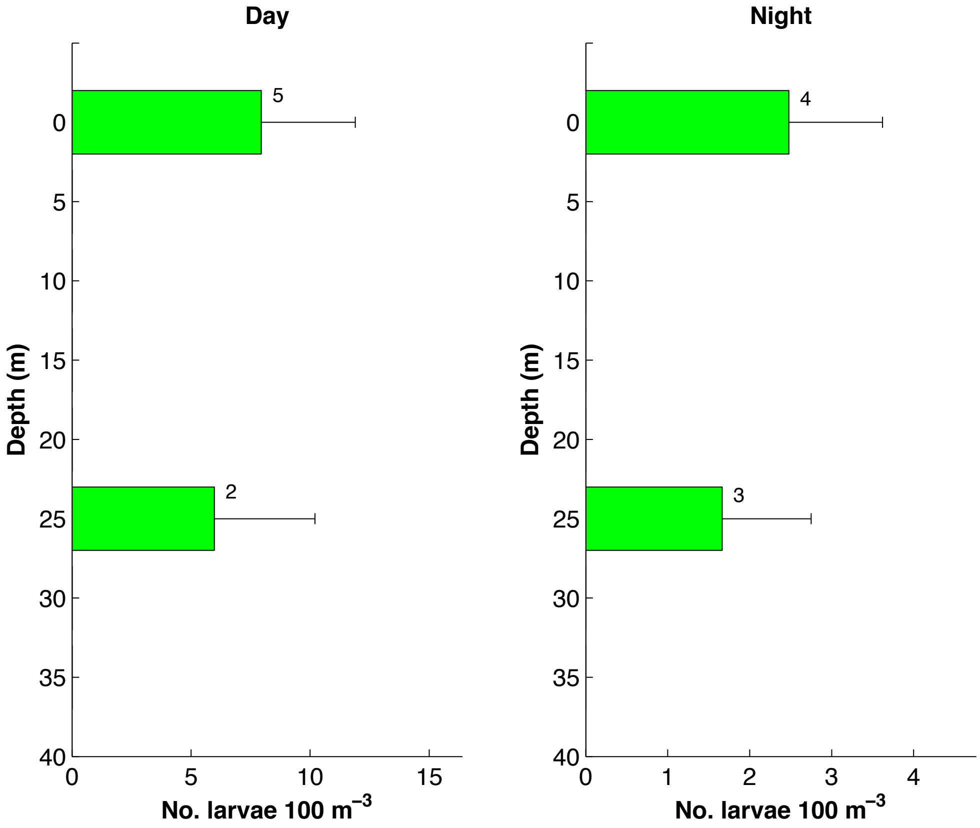
15 **Bipinnaria larva**



16

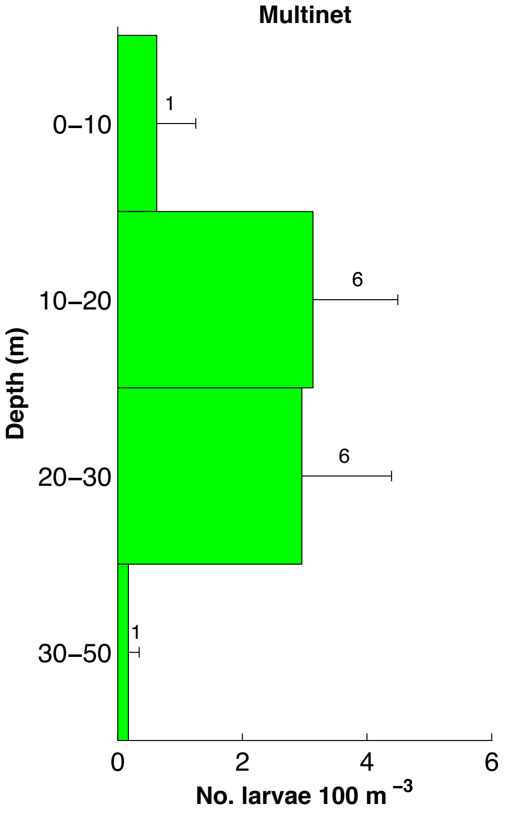
Brachiolaria larva





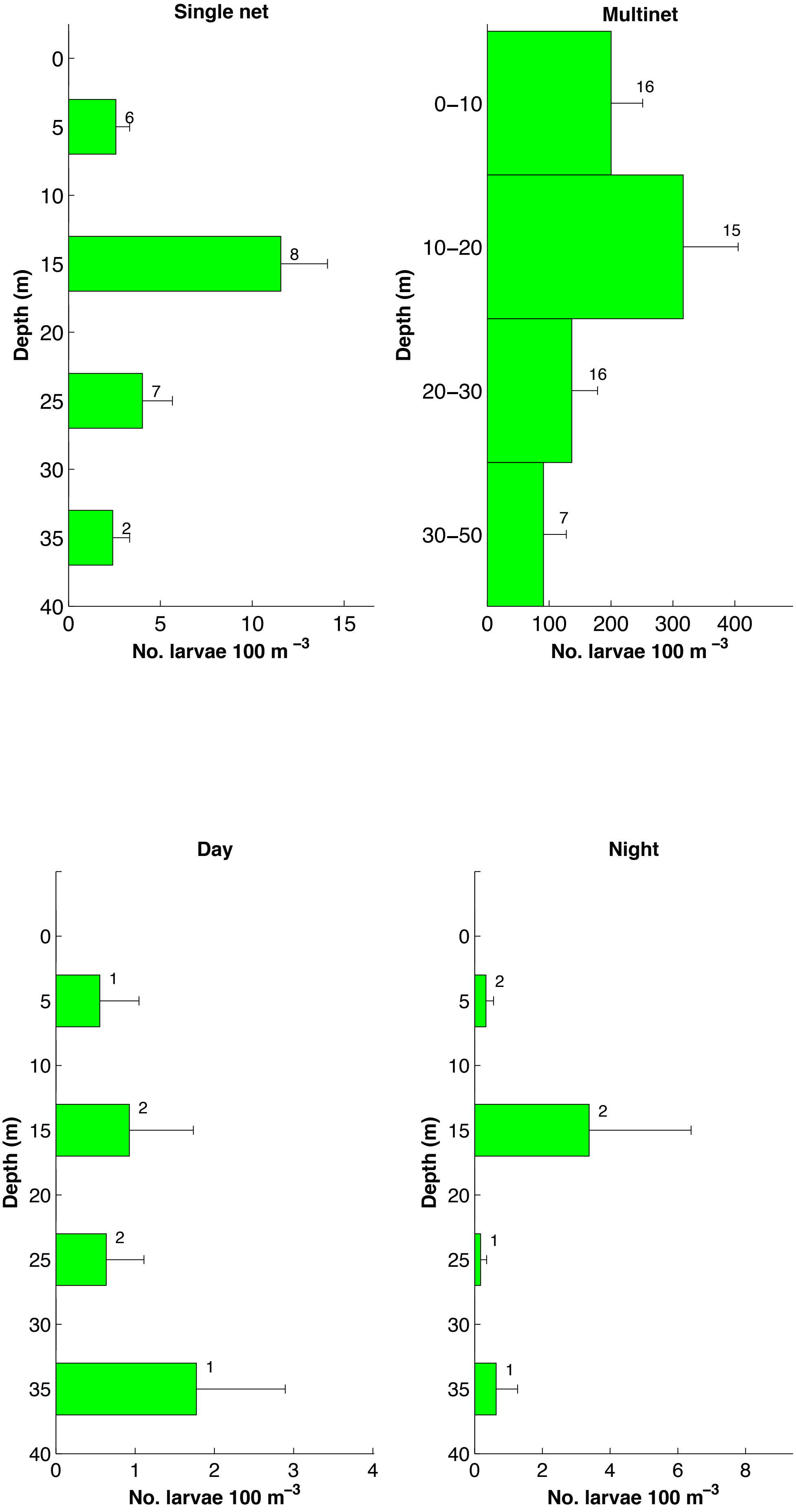
17

Luidia sarsi

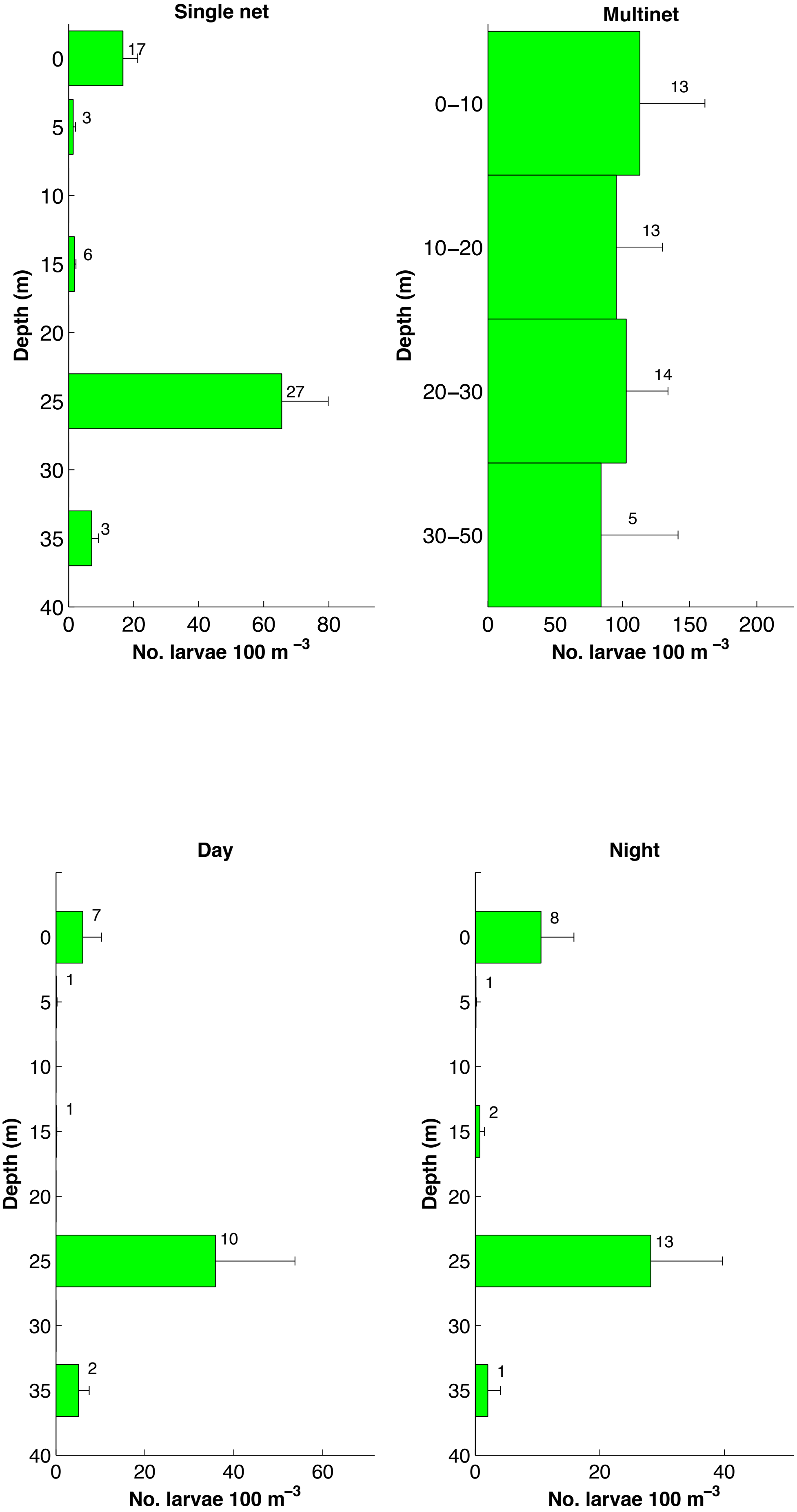


18

Naplius larva

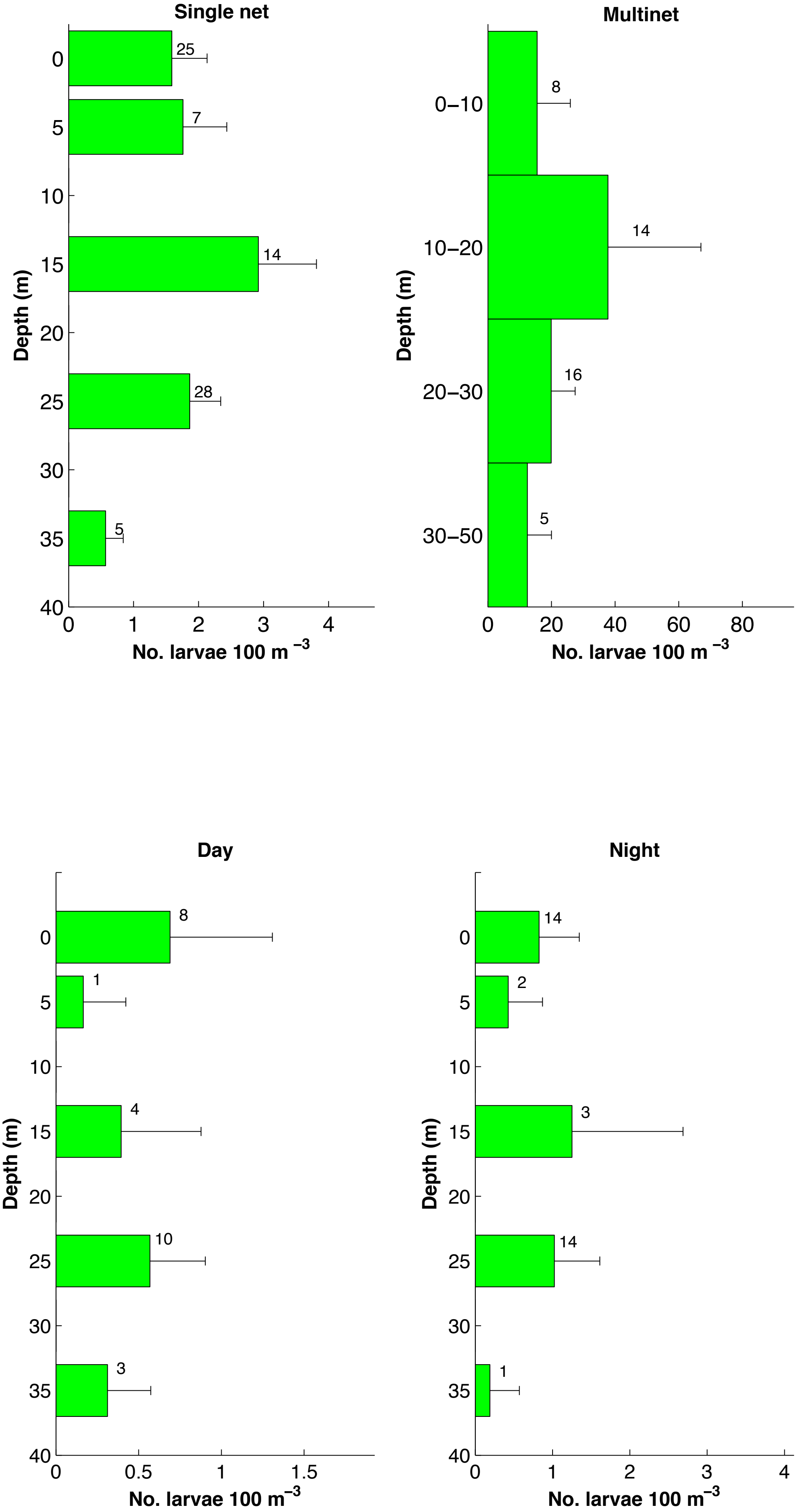


19 **Cyprid larva**



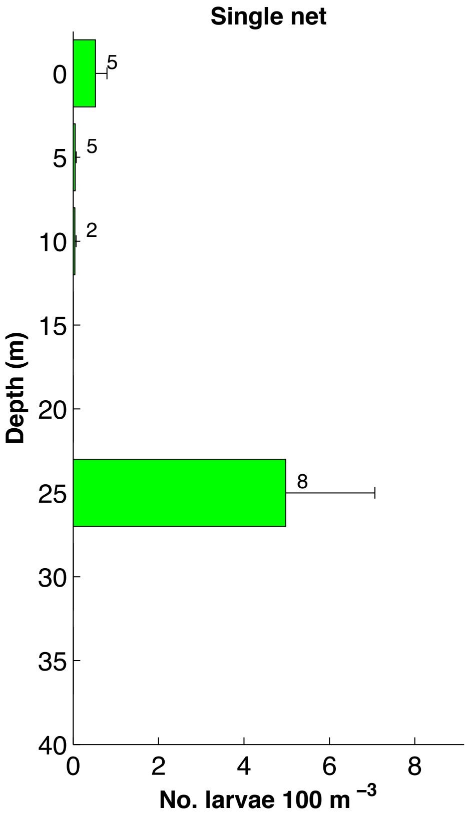
20

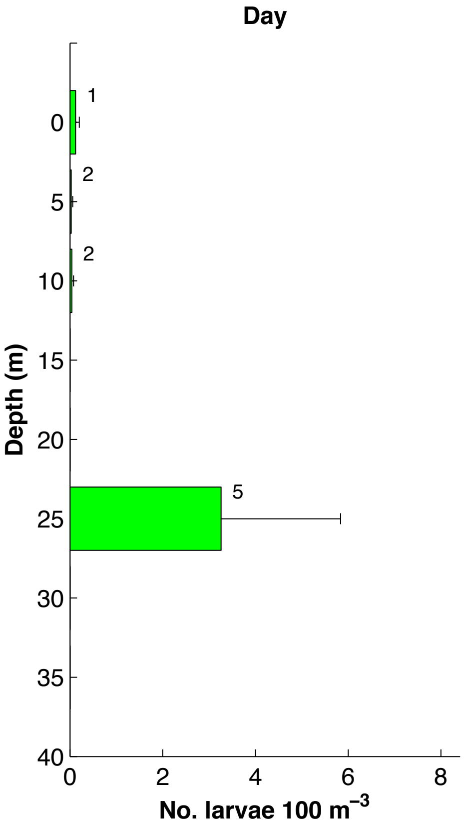
Caridea spp. Z

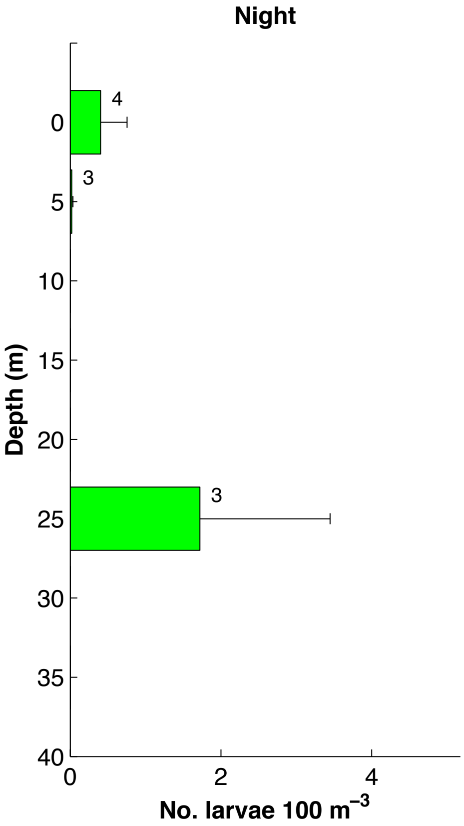


21

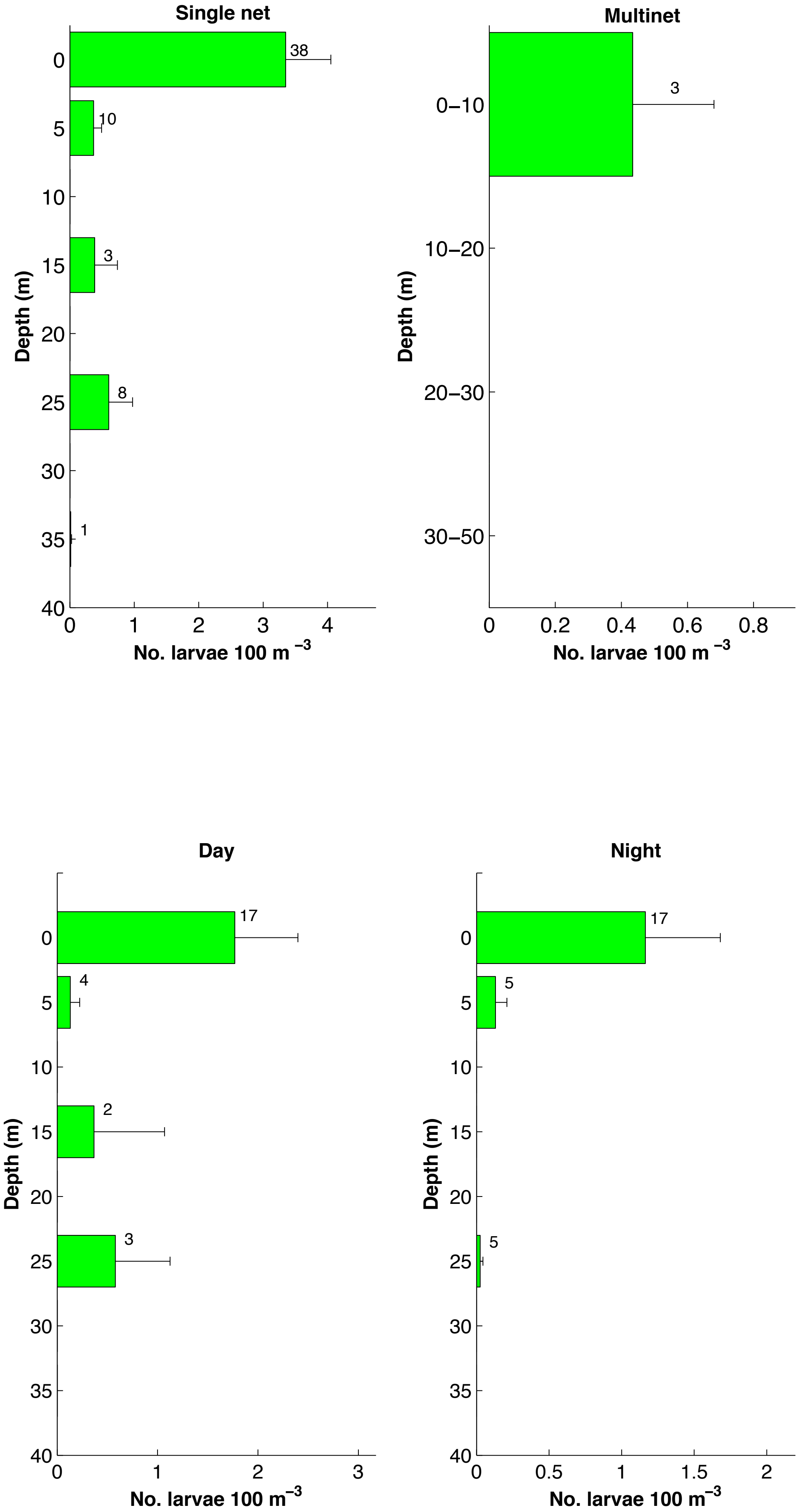
Palaemon sp. Z1–2







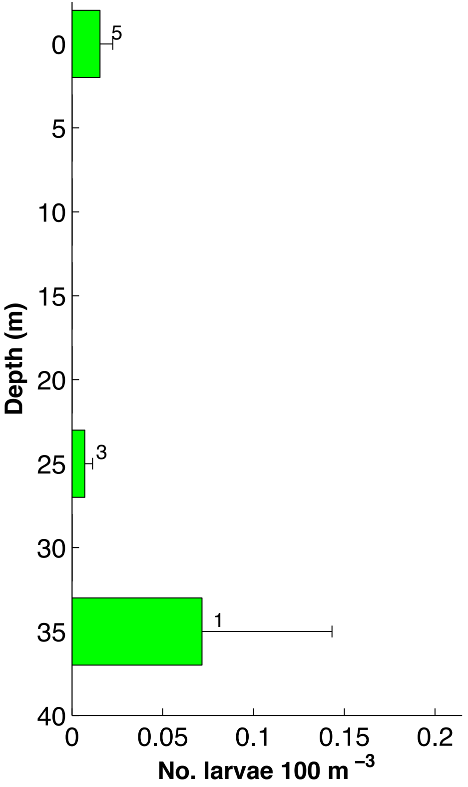
Palaemon sp. Z3–5



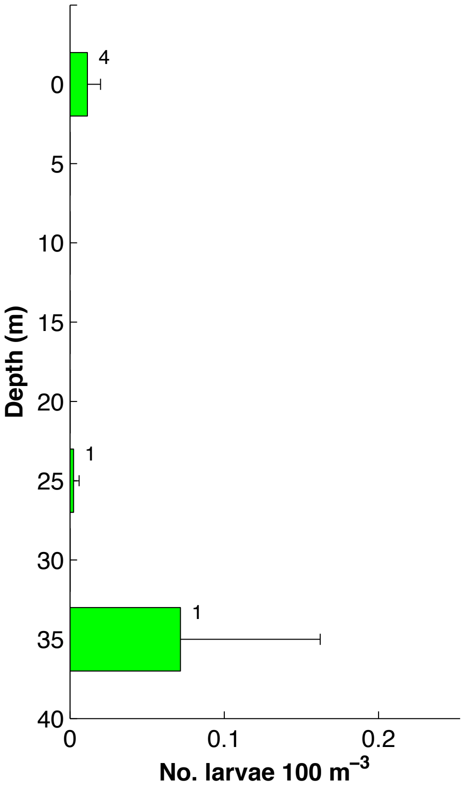
23

Palaemon sp. PL

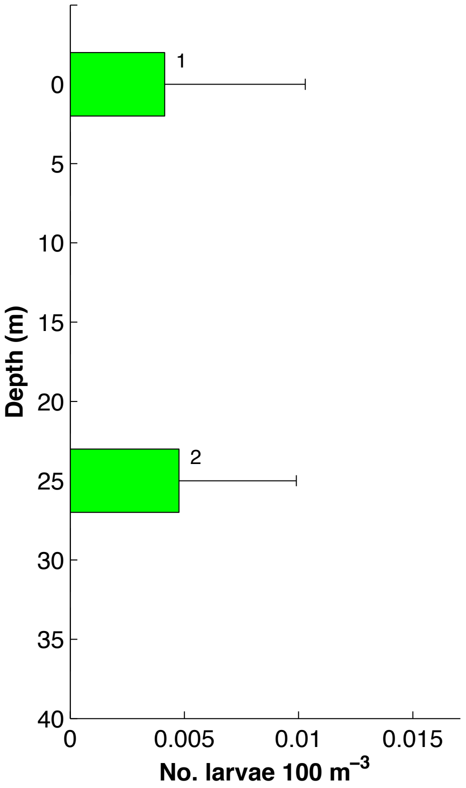
Single net



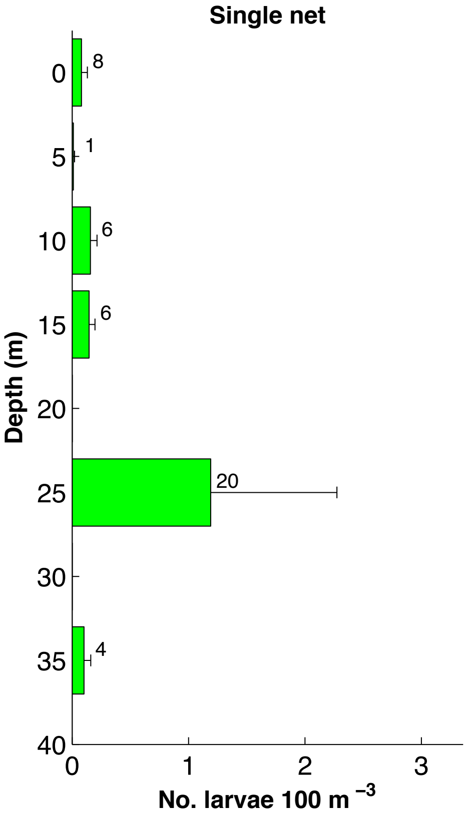
Day

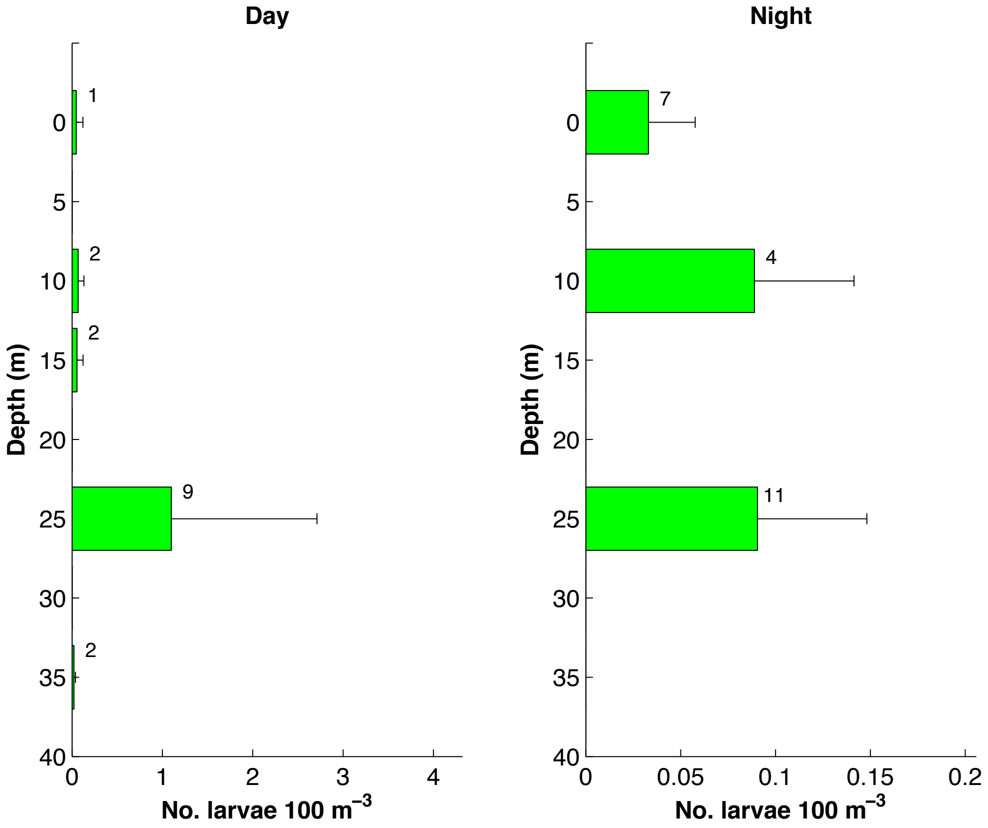


Night



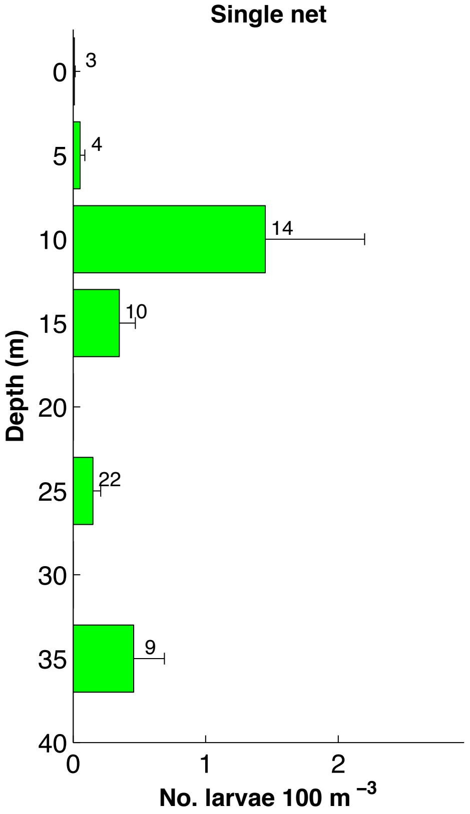
Crangon sp. Z1–3

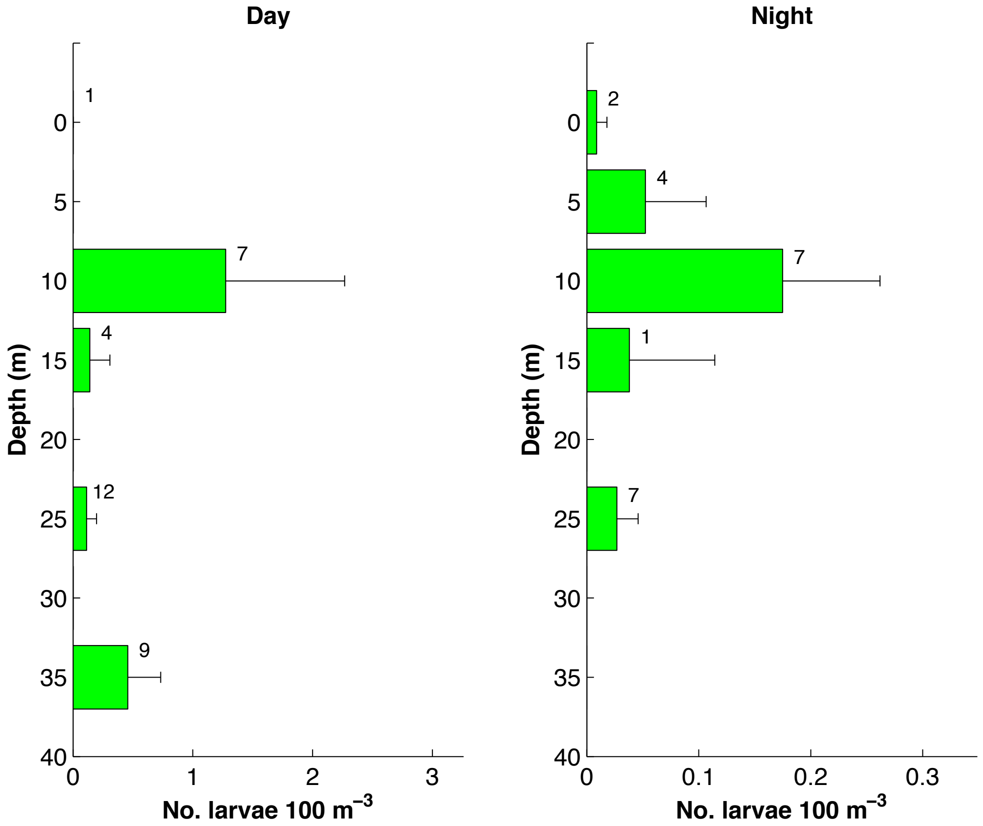




25

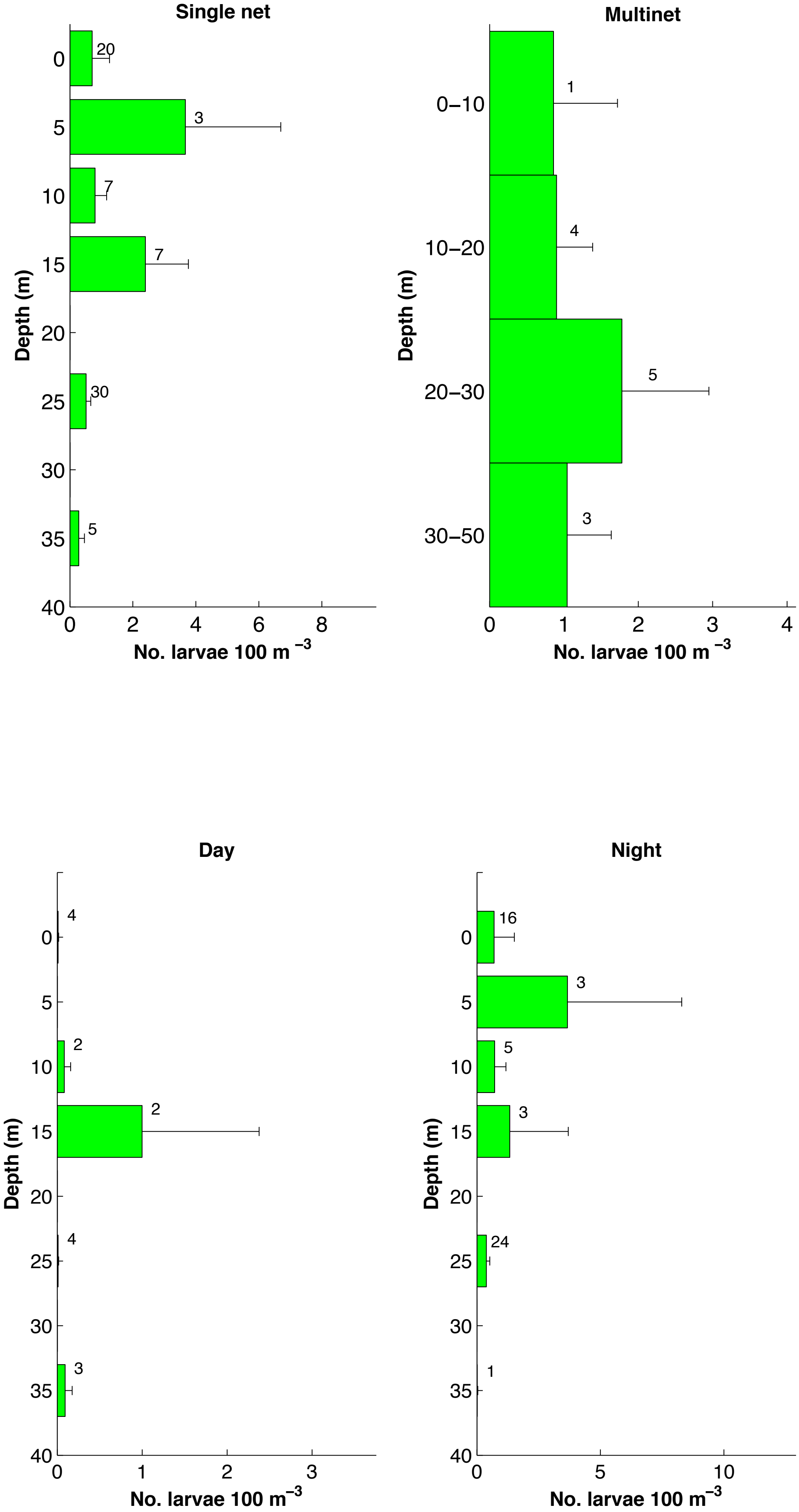
Crangon sp. Z4–5





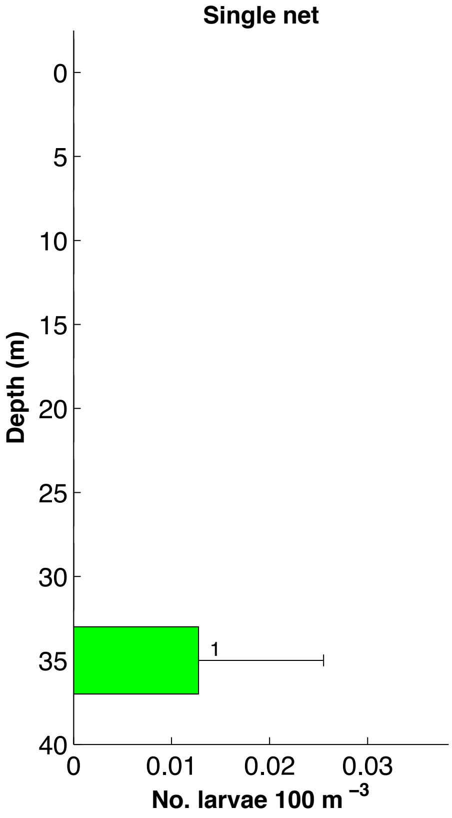
26

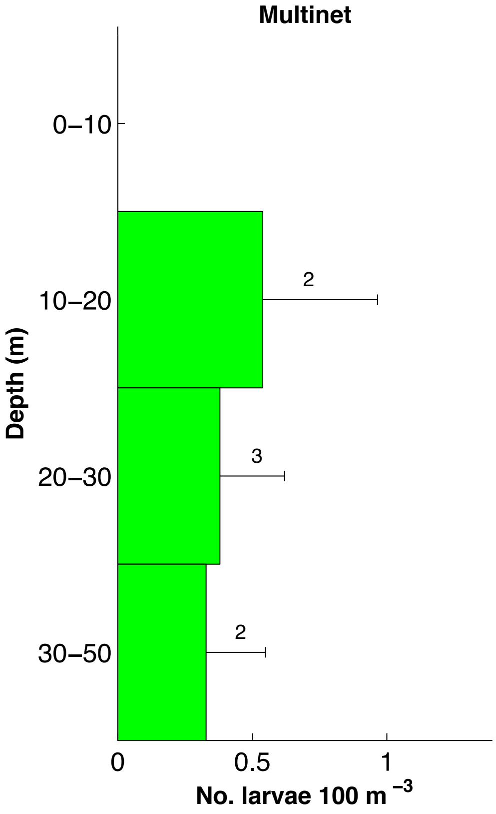
Crangon sp. PL

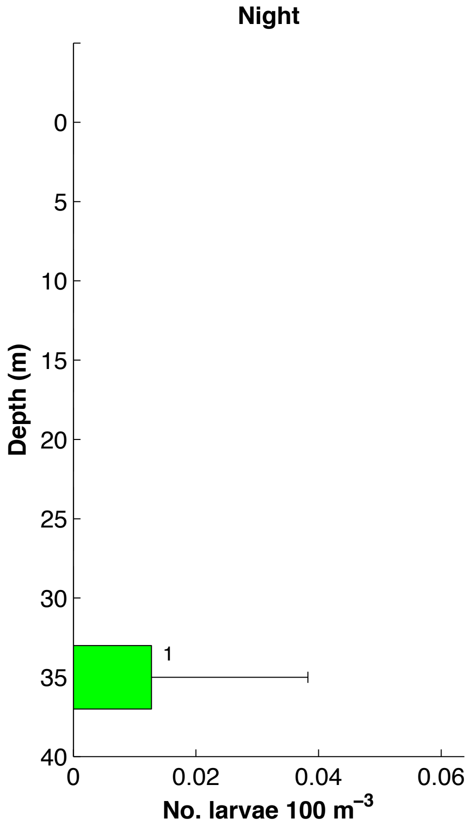


27

Philicheras bispinosus Z

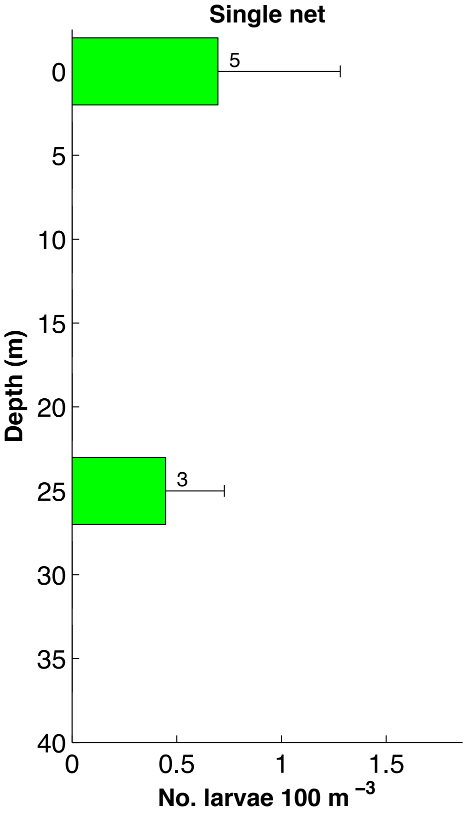


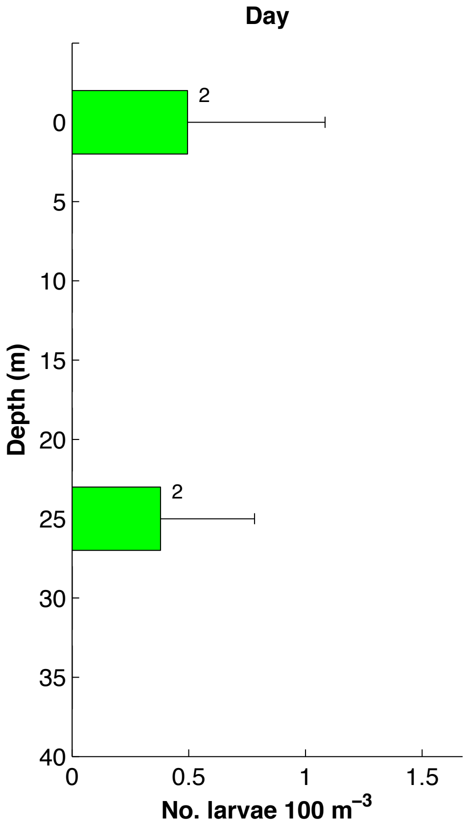


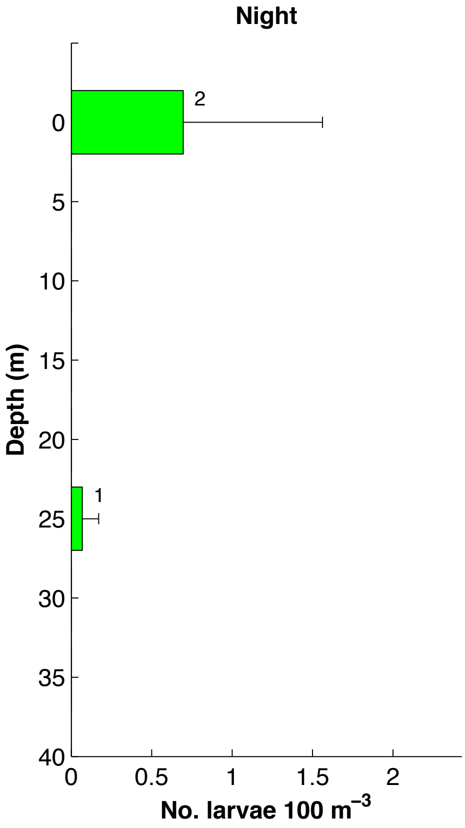


28

Pand ZI–V

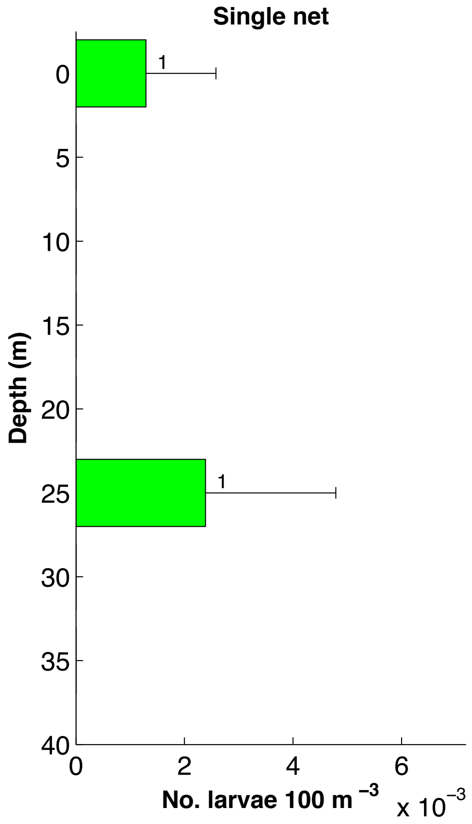

Single net
Depth (m)
0
5
10
15
20
25
30
35
40
5
3
0
0.5
1
1.5
No. larvae 100 m $^{-3}$

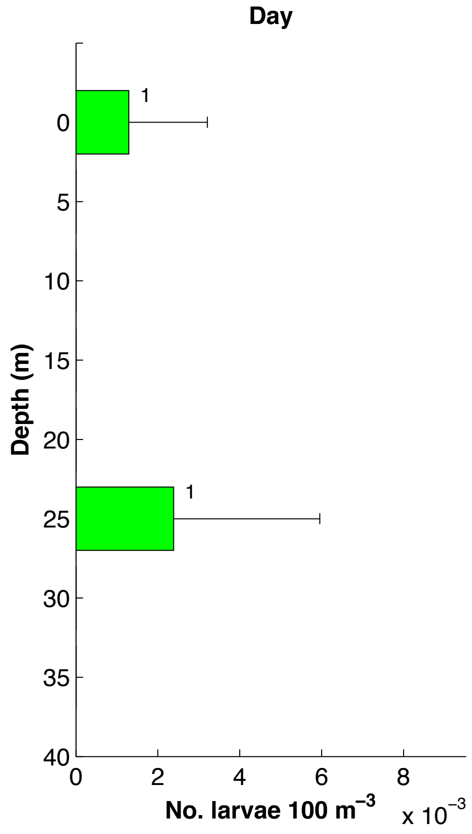

Day
Depth (m)
0
5
10
15
20
25
30
35
40
2
2
0
0.5
1
1.5
No. larvae 100 m^{-3}


Night
Depth (m)
0
5
10
15
20
25
30
35
40
2
1
0
0.5
1
1.5
2
No. larvae 100 m^{-3}

29

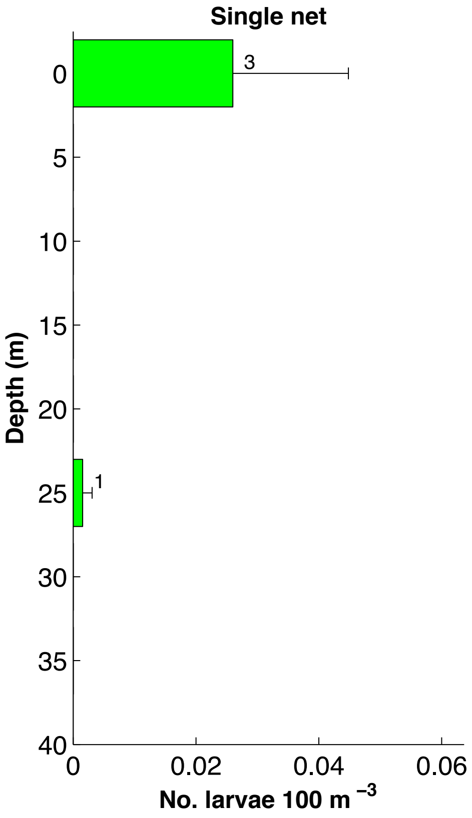
Pandalina brevirostus Z

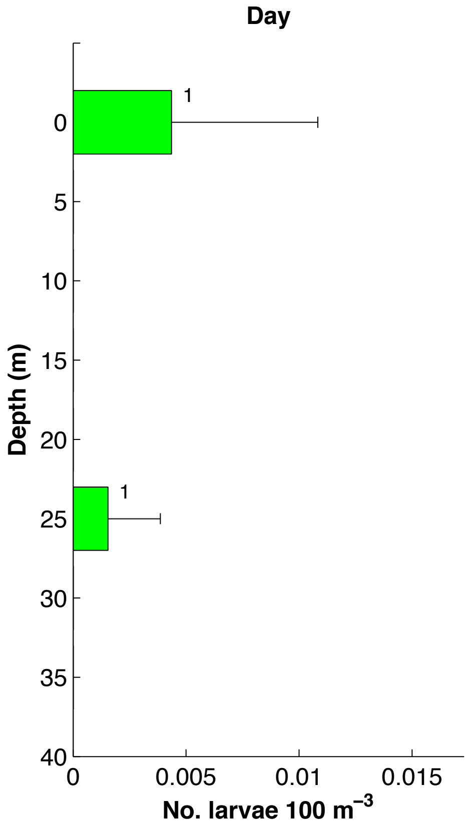


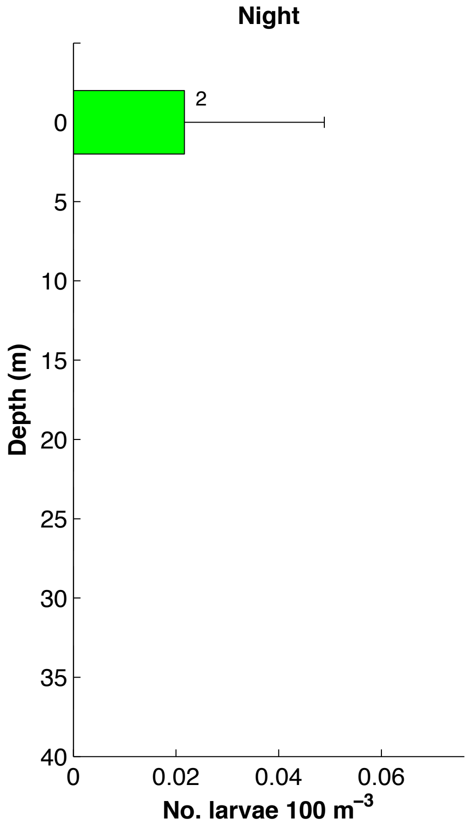


30

Athanas nitescens (cf.) PL

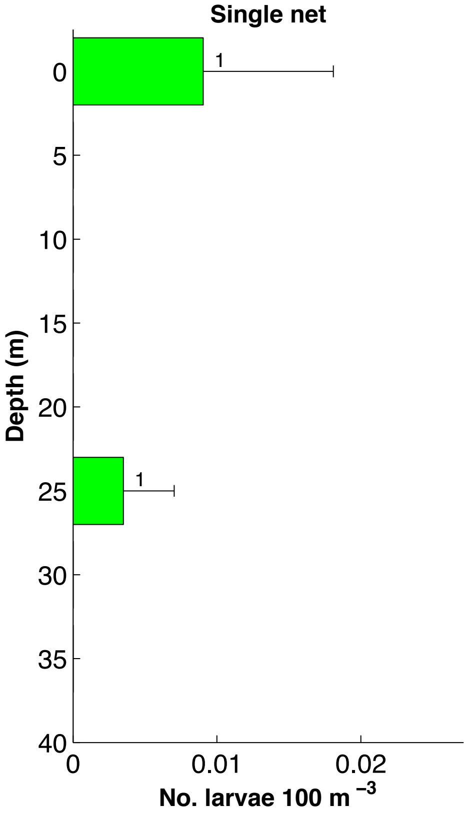


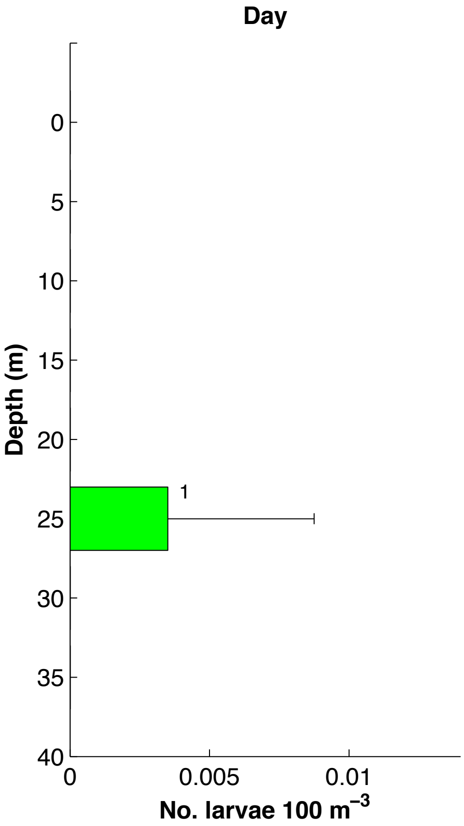


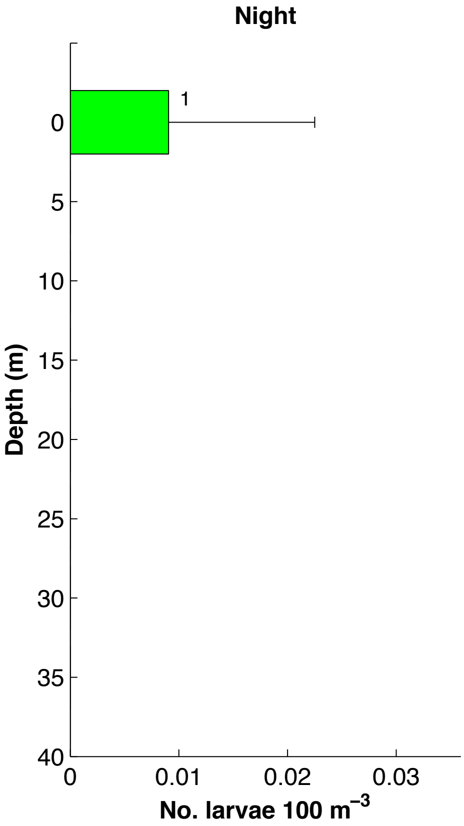


31

Alphaeid Z

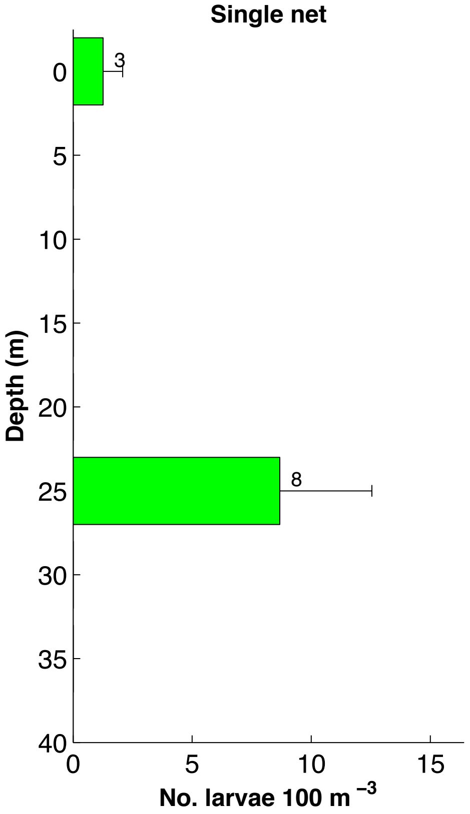


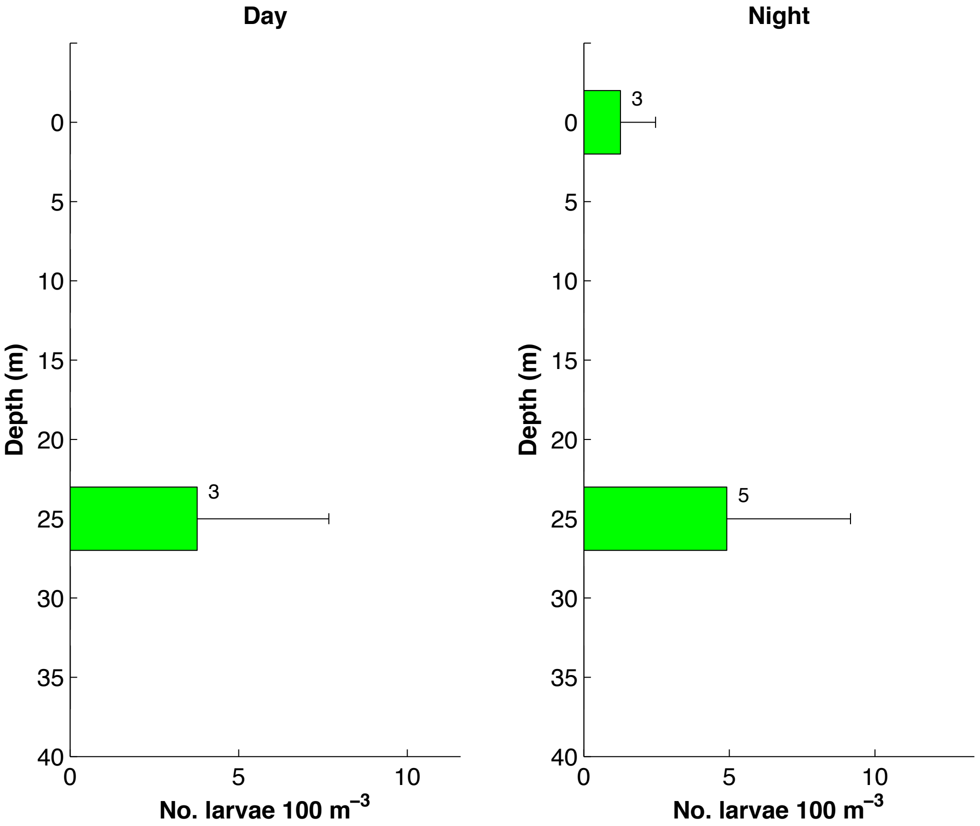




32

Hippolythid Z

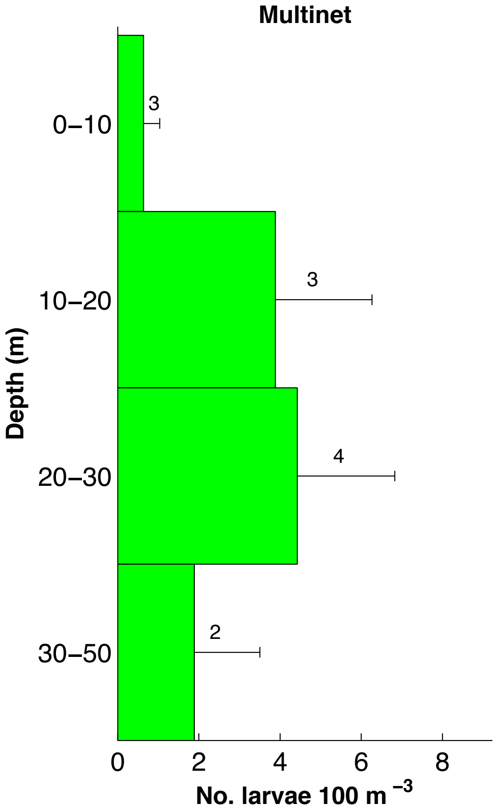

Single net


Day

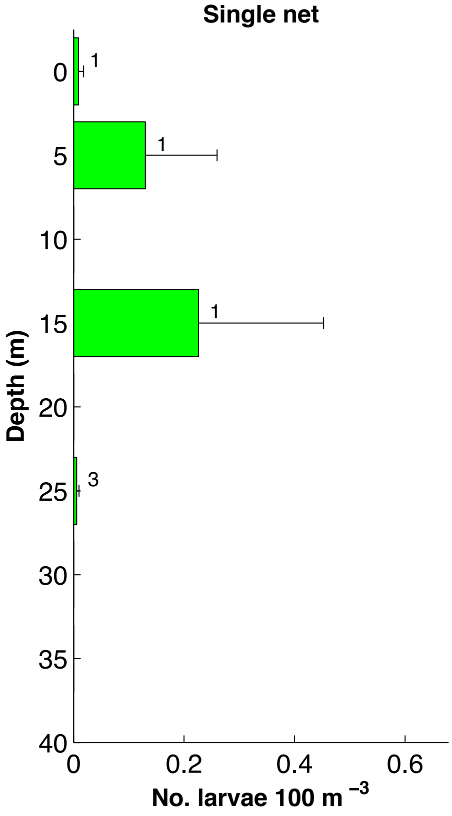
Night

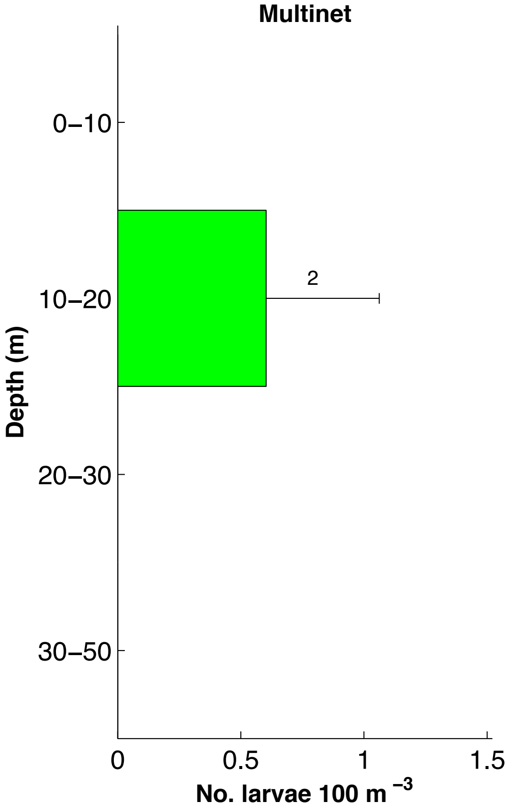
33

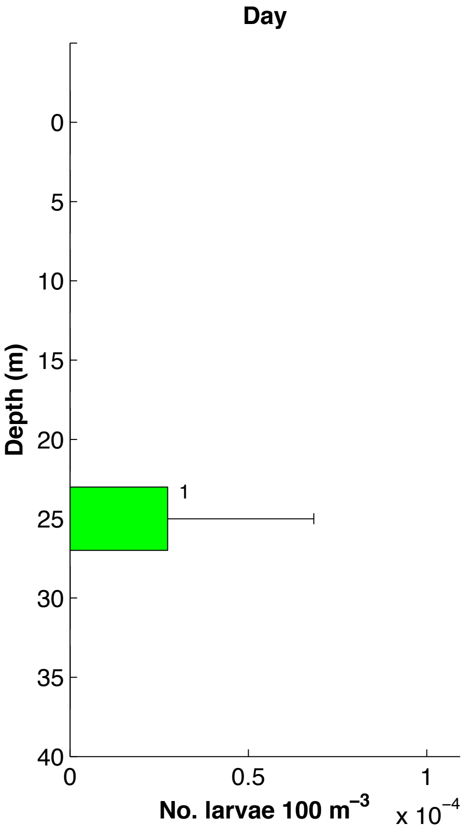
Callianassa sp. Z

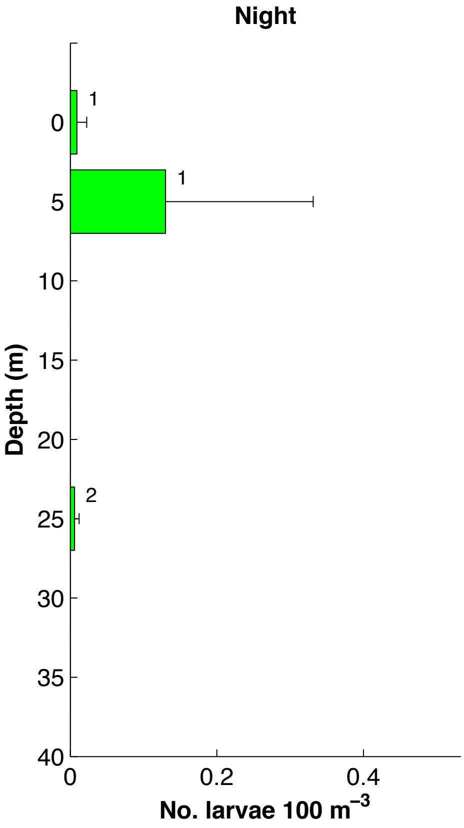


Upogebia sp. Z





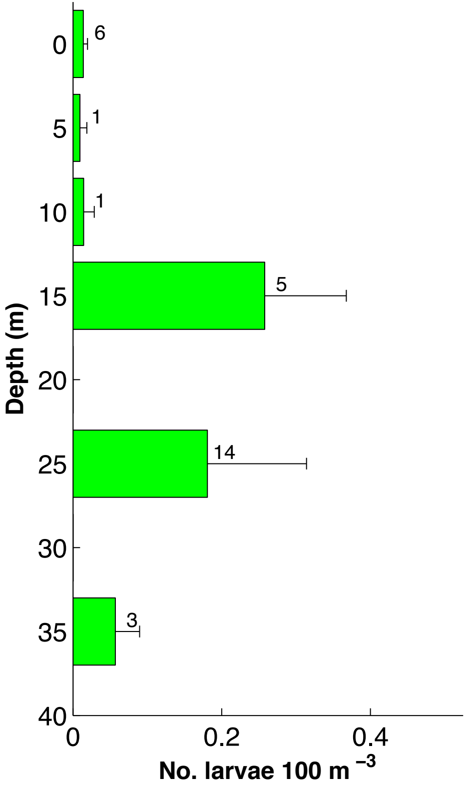


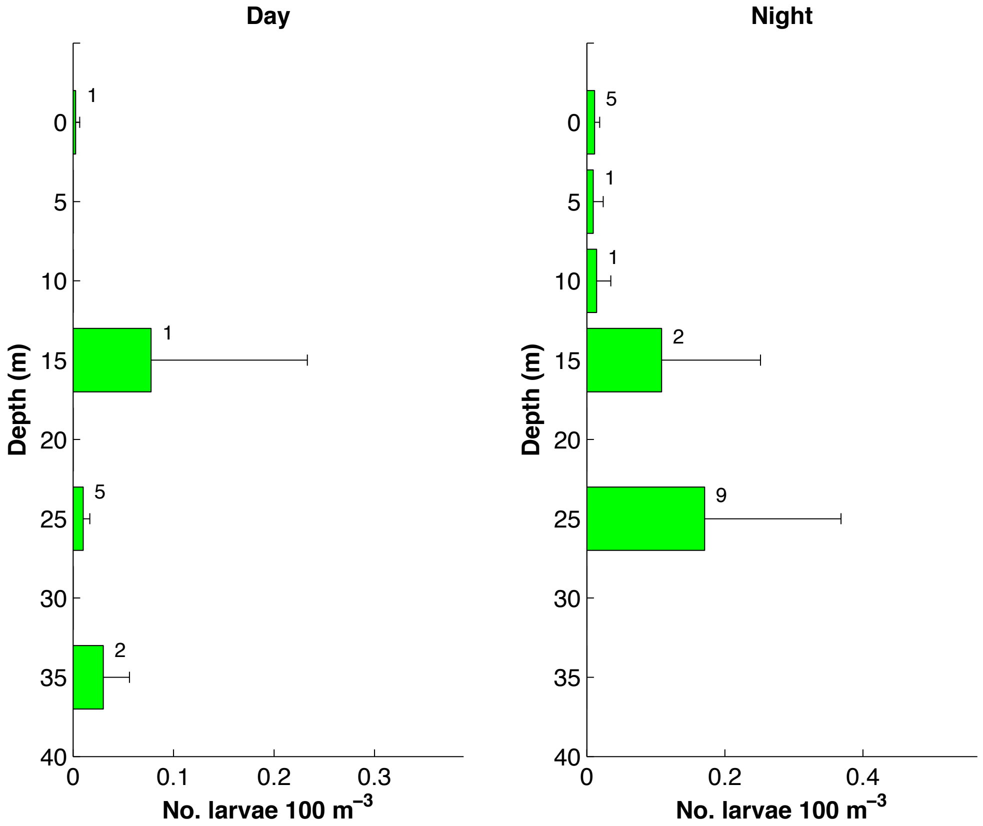


35

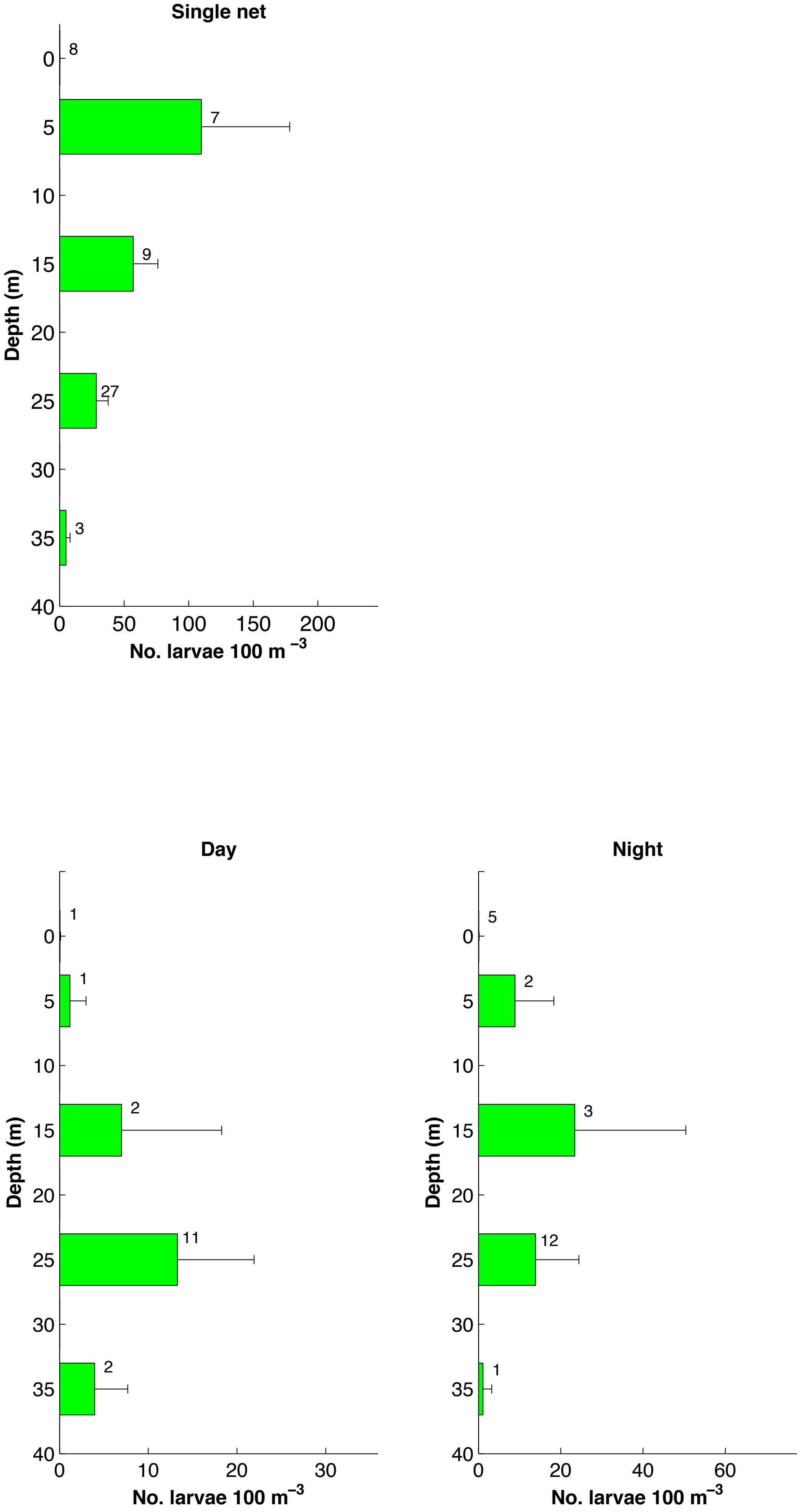
Upogebia sp. PL

Single net





Calocaris sp. Z



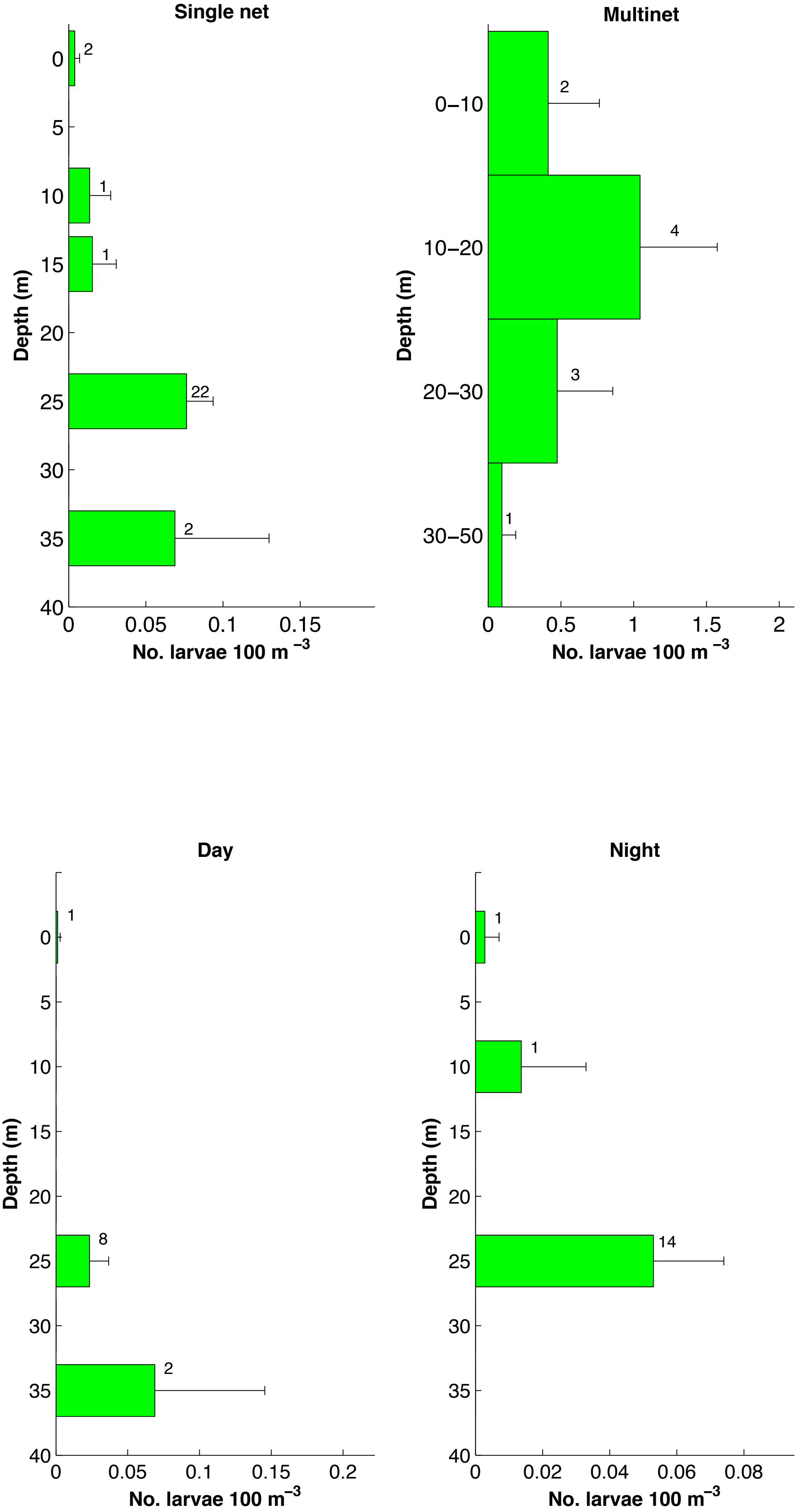
Single net

Day

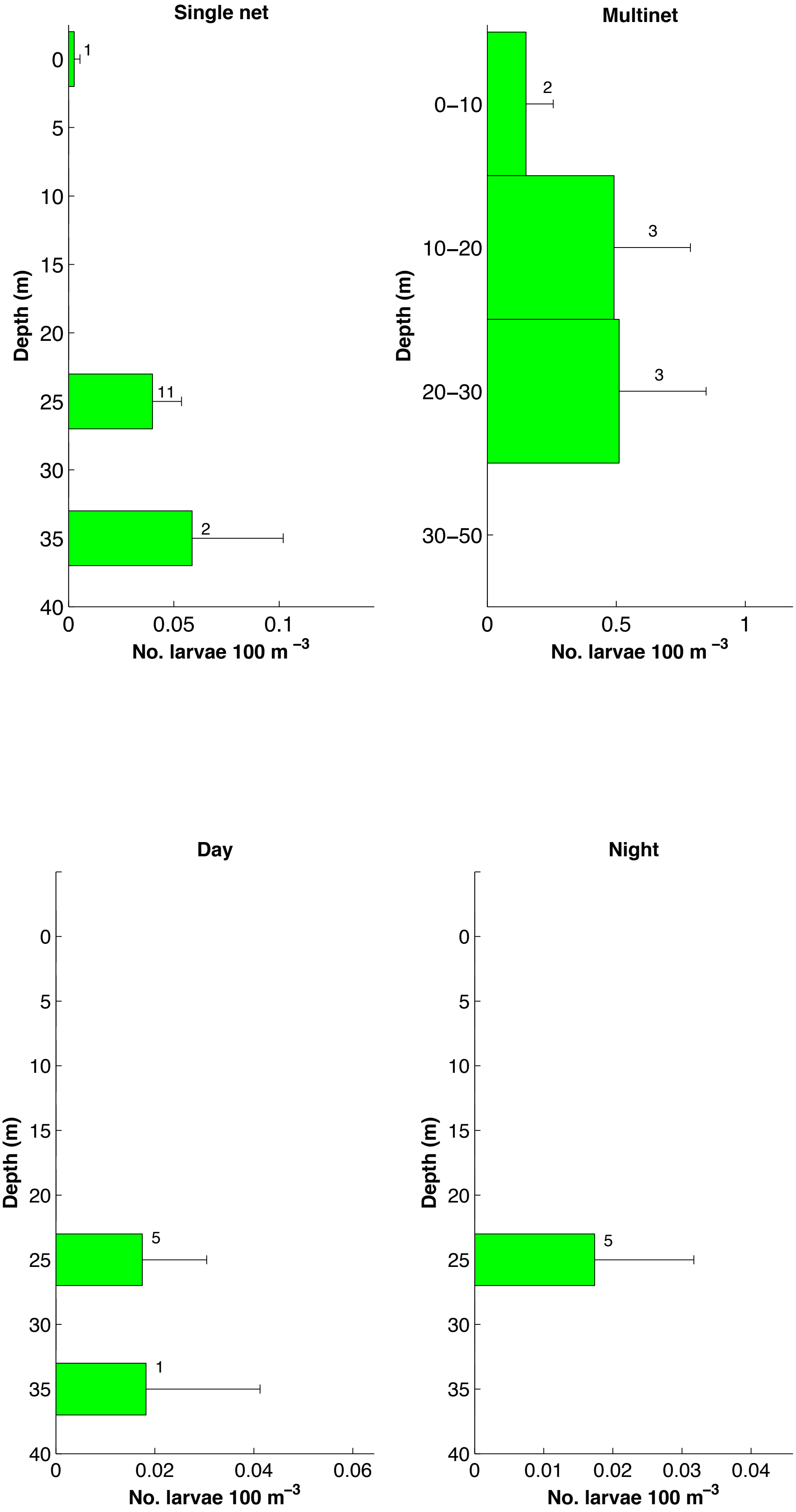
Night

37

Nephrops norvegicus Z1−2

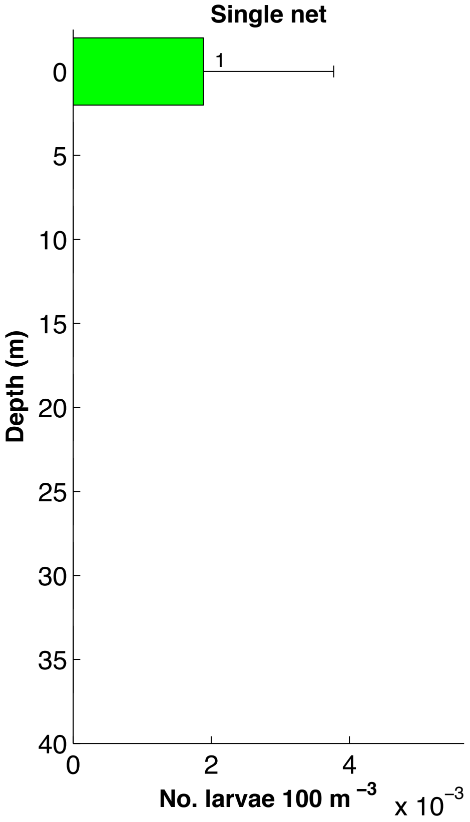


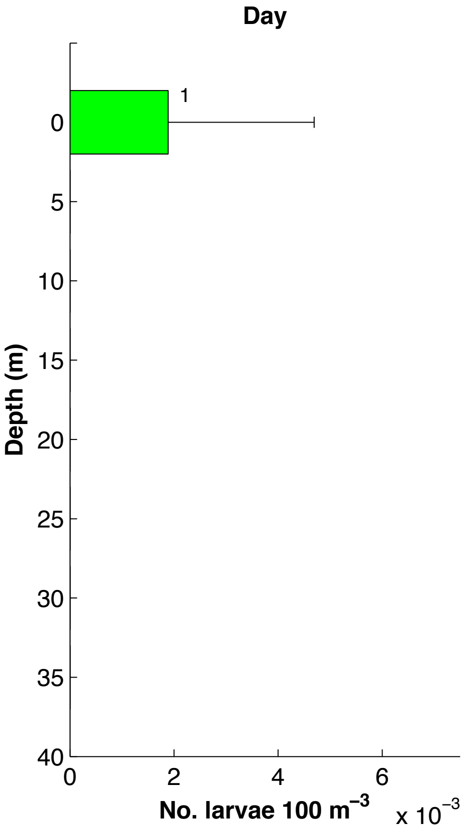
Nephrops norvegicus Z3–5



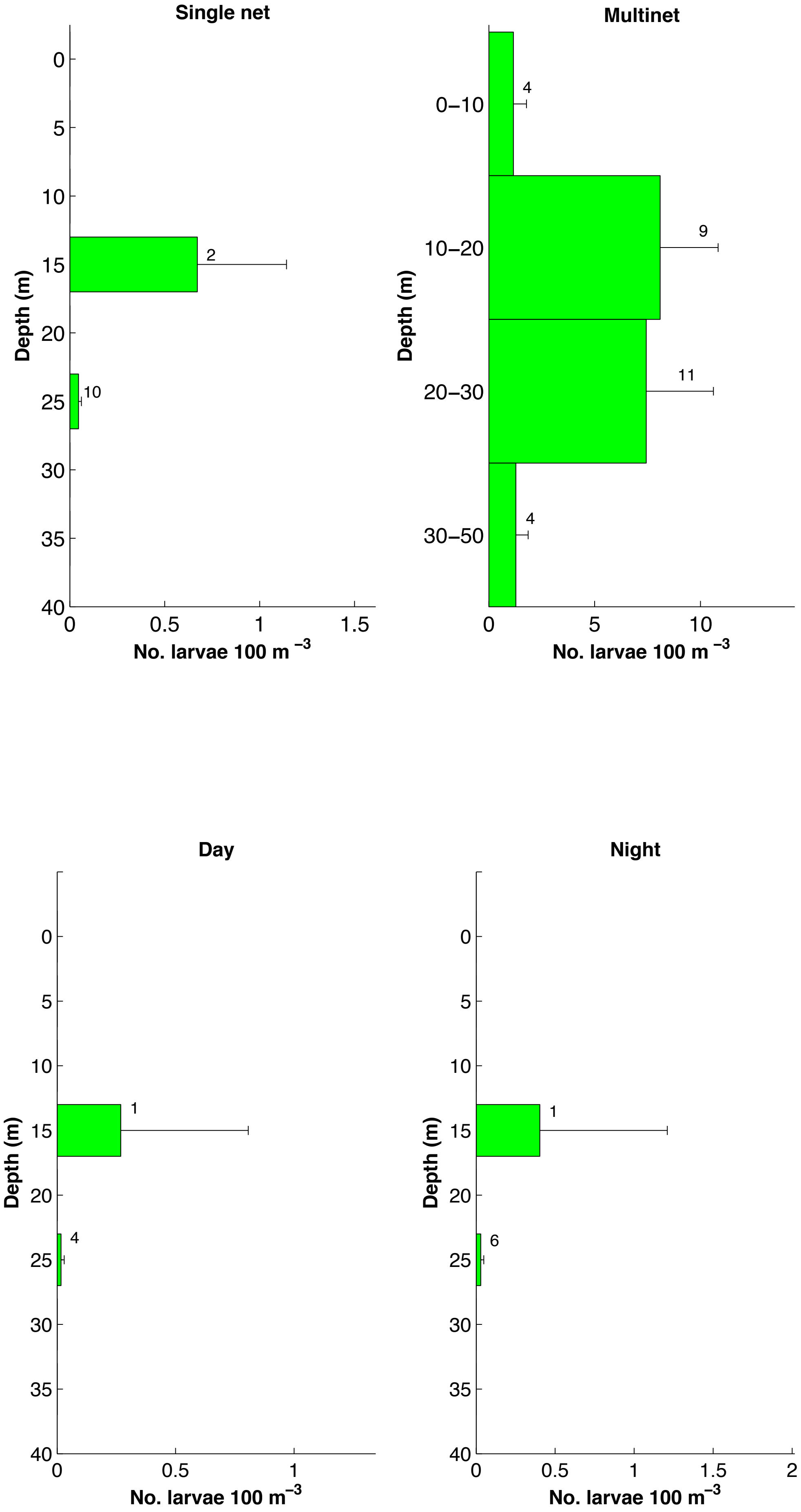
39

Homarus gammarus Z1



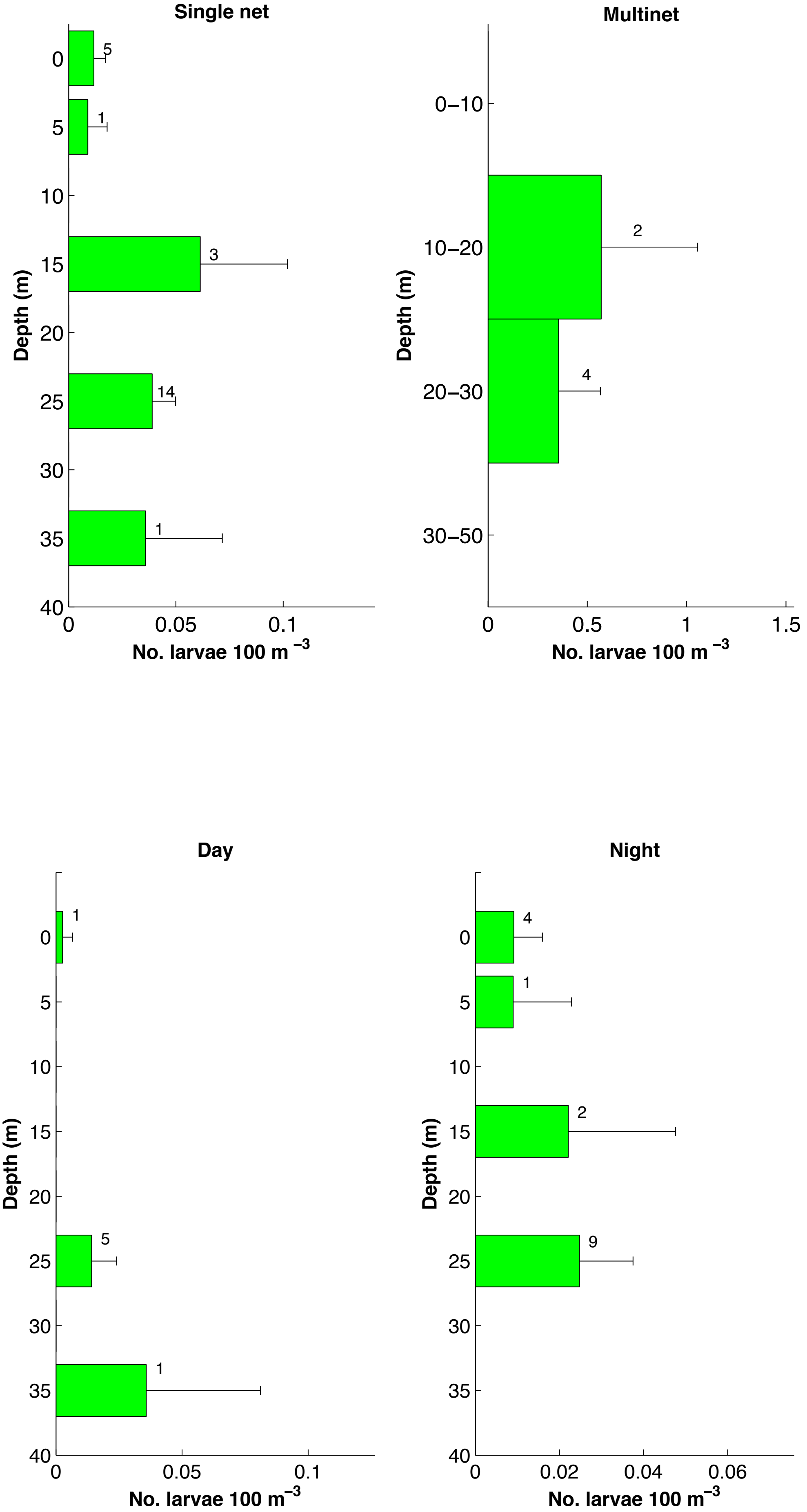


Pagurid Z1–5

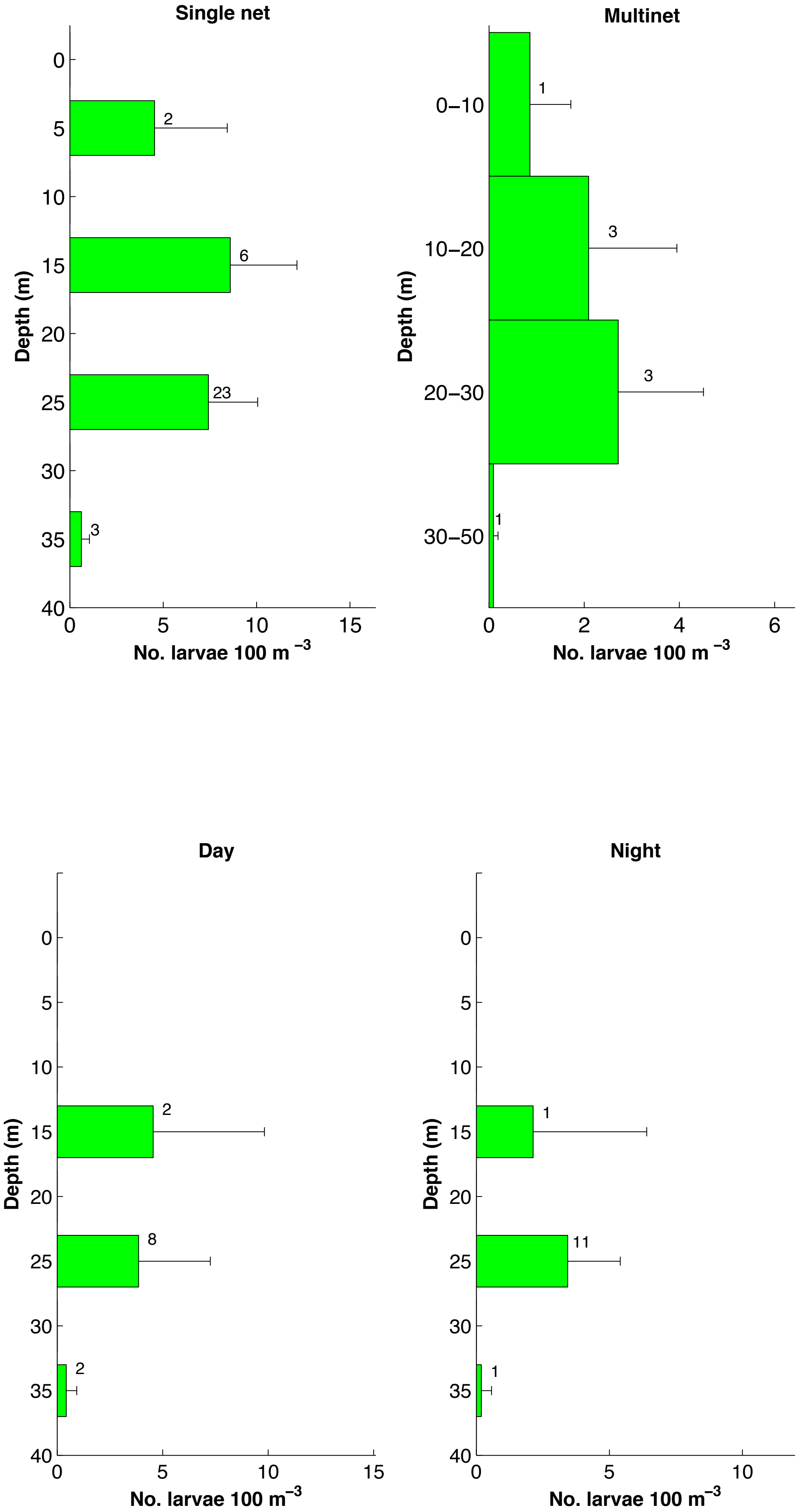

Single net
Depth (m)
0
5
10
15
20
25
30
35
40
2
10
0
0.5
1
1.5
No. larvae 100 m −3
Multinet
Depth (m)
0–10
10–20
20–30
30–50
4
9
11
4
0
5
10
No. larvae 100 m −3
Day
Depth (m)
0
5
10
15
20
25
30
35
40
1
4
0
0.5
1
No. larvae 100 m−3
Night
Depth (m)
0
5
10
15
20
25
30
35
40
1
6
0
0.5
1
1.5
2
No. larvae 100 m−3

41

Pagurid PL



Galathea sp. Z



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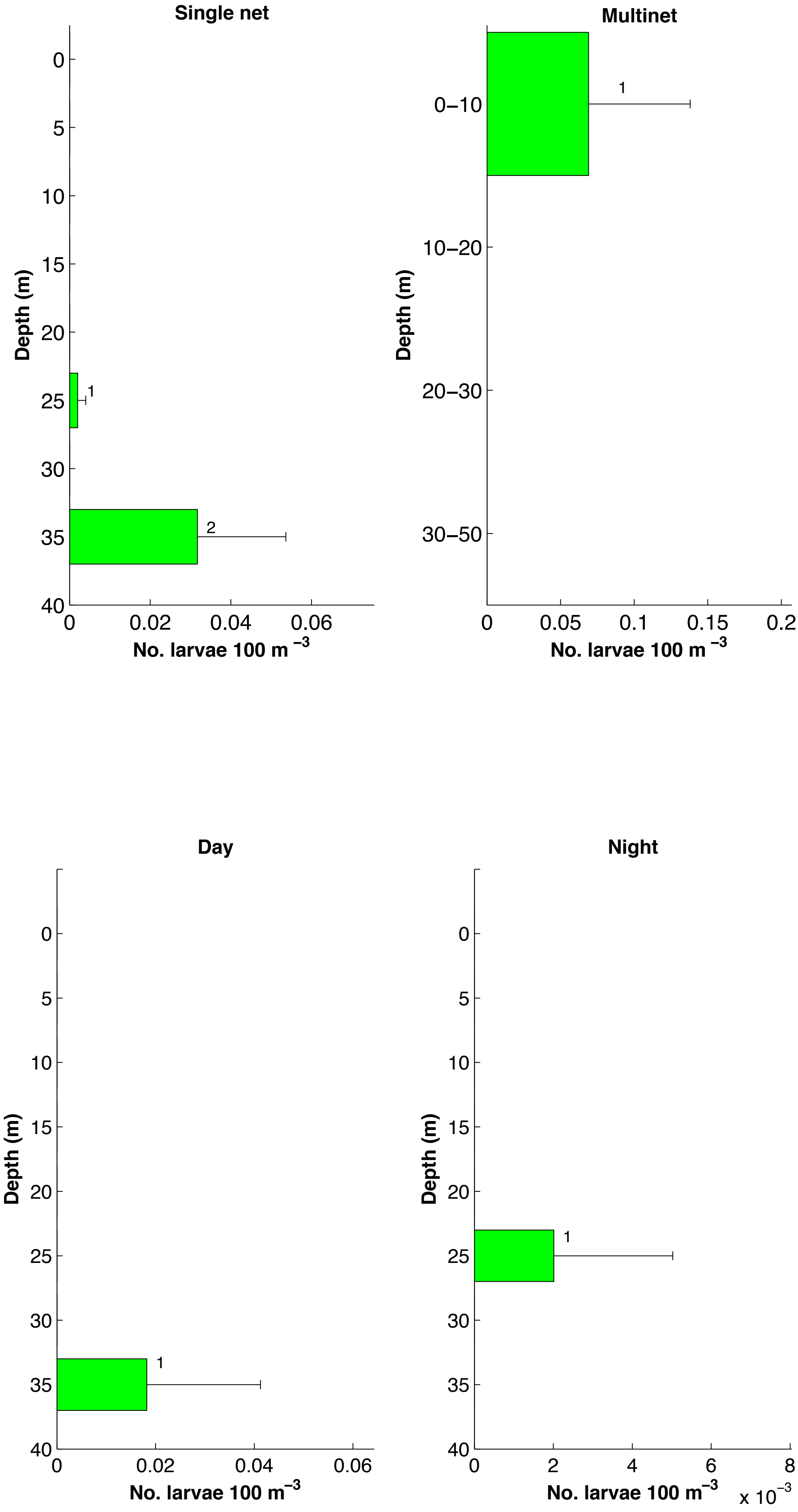
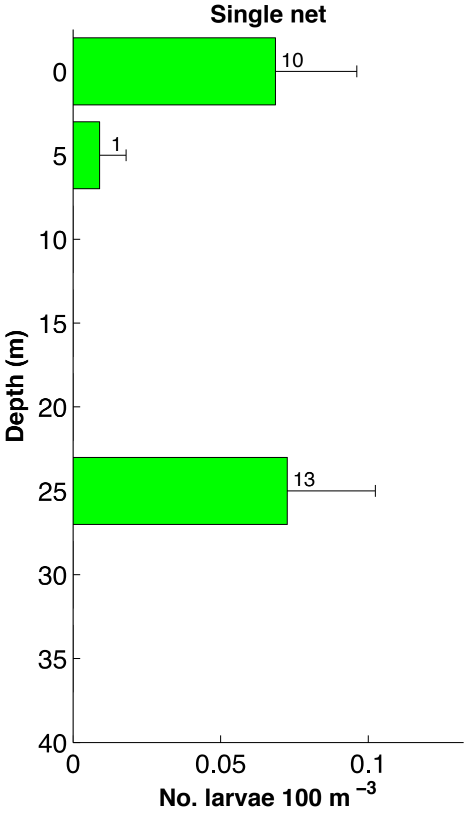
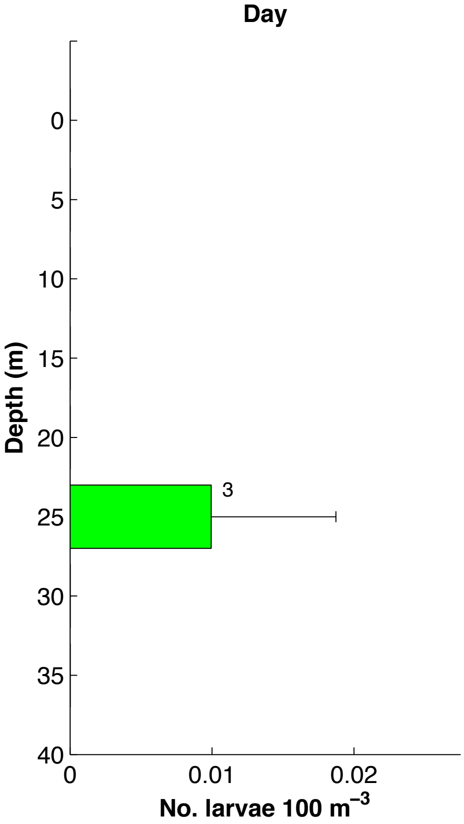
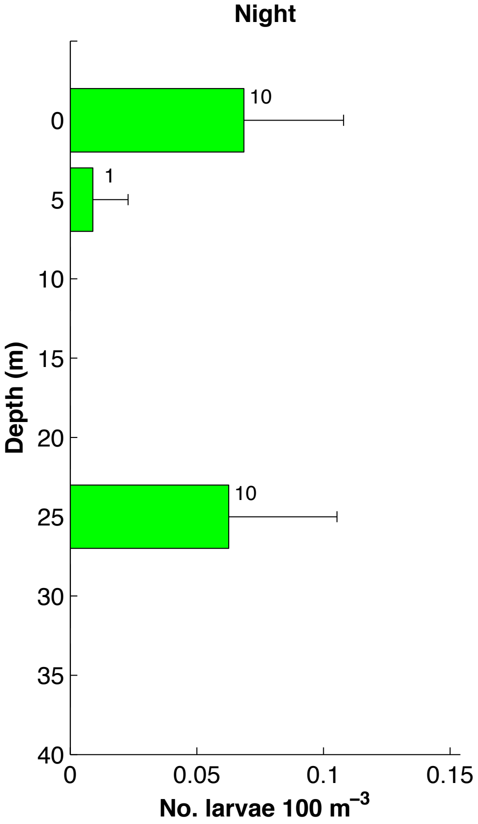
Galathea sp. PL



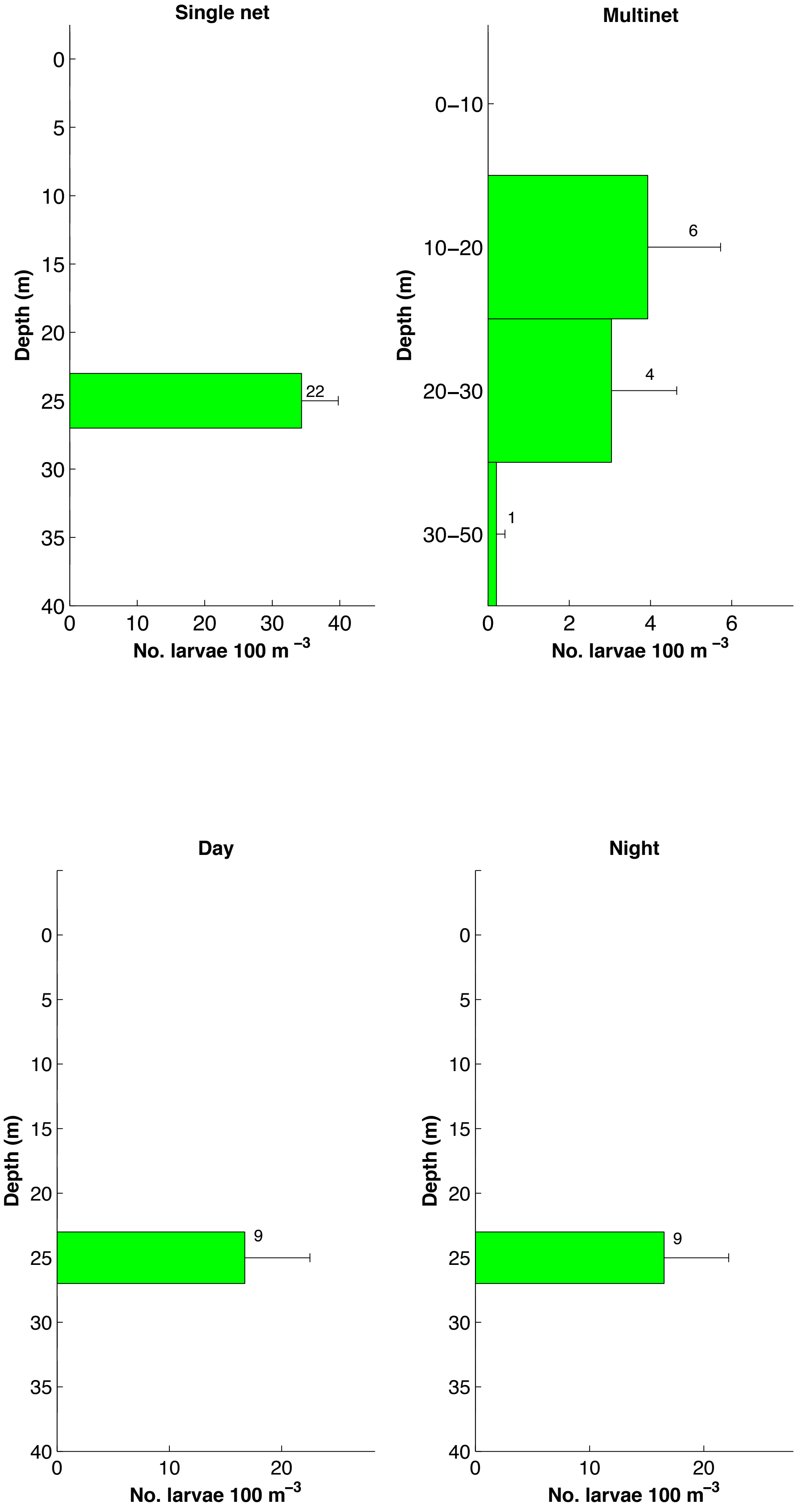
Munidopsis sp. PL



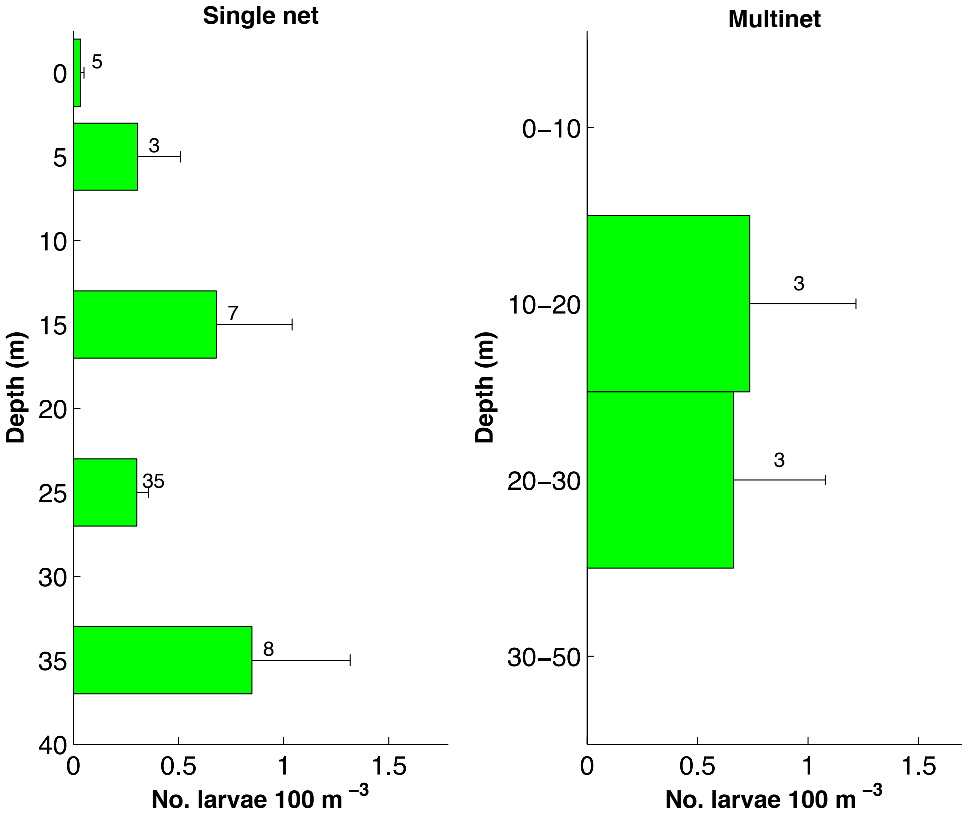


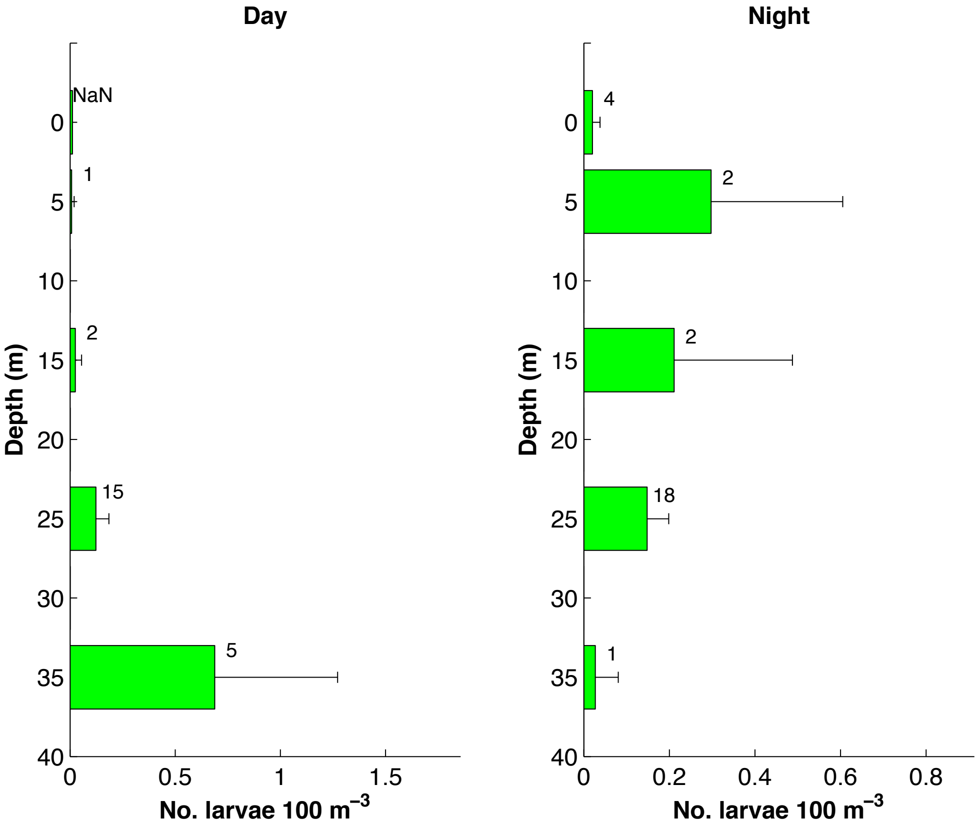


45 Pisidia longicornis (cf.) Z



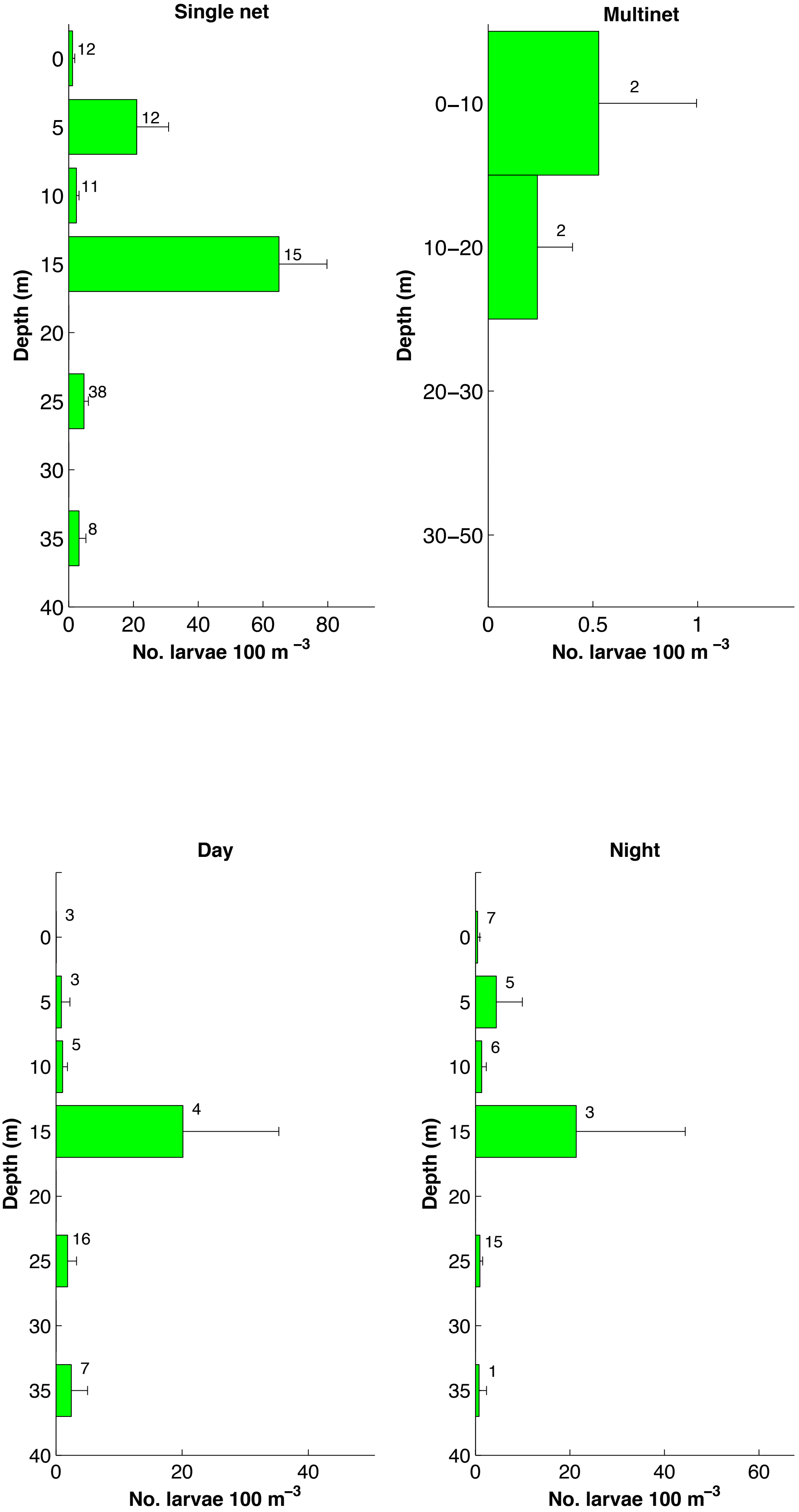
Pisidia longicornis (cf.) PL



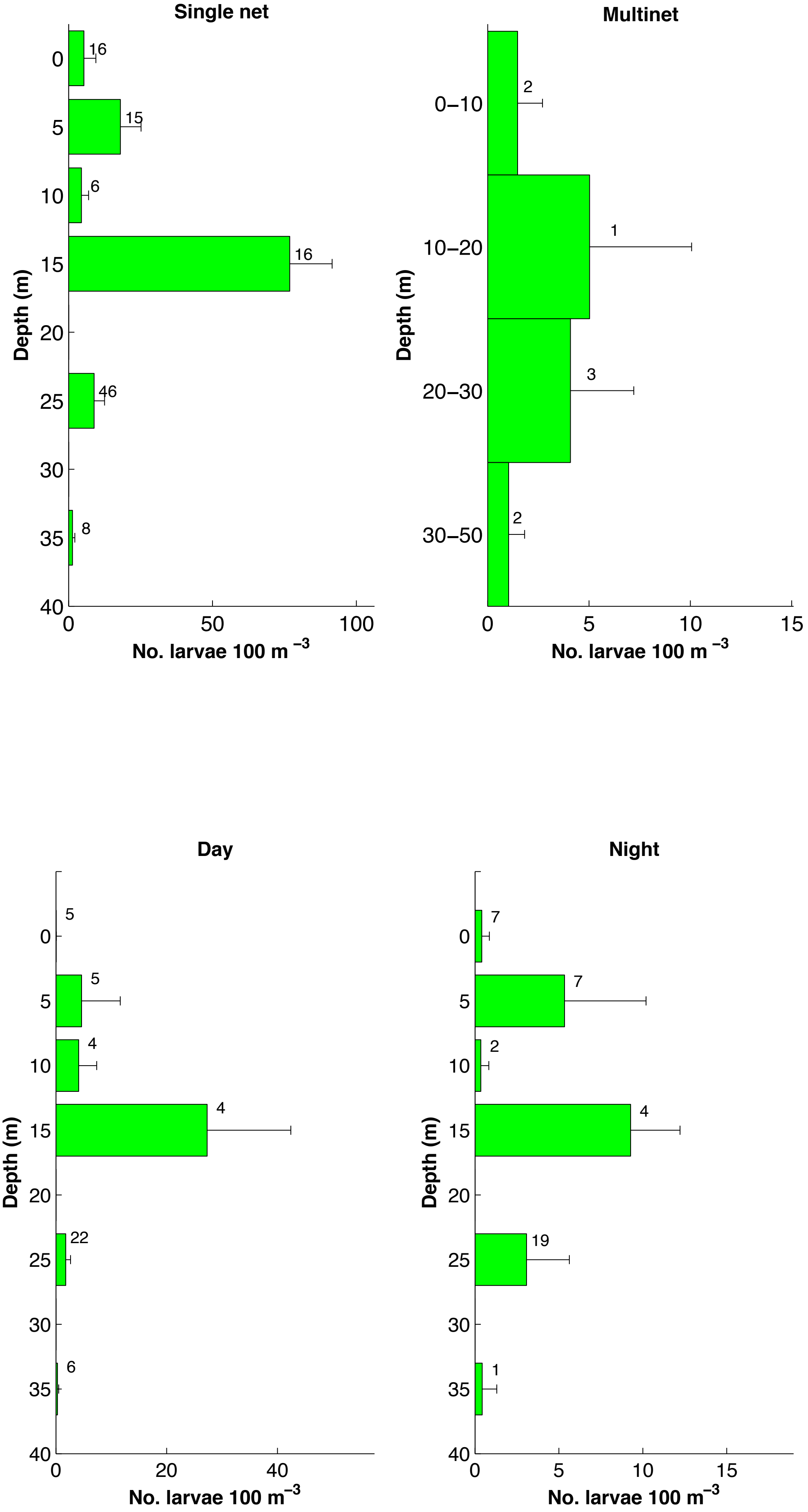


47

Carcinus maenas Z1–2



Carcinus maenas Z3–4



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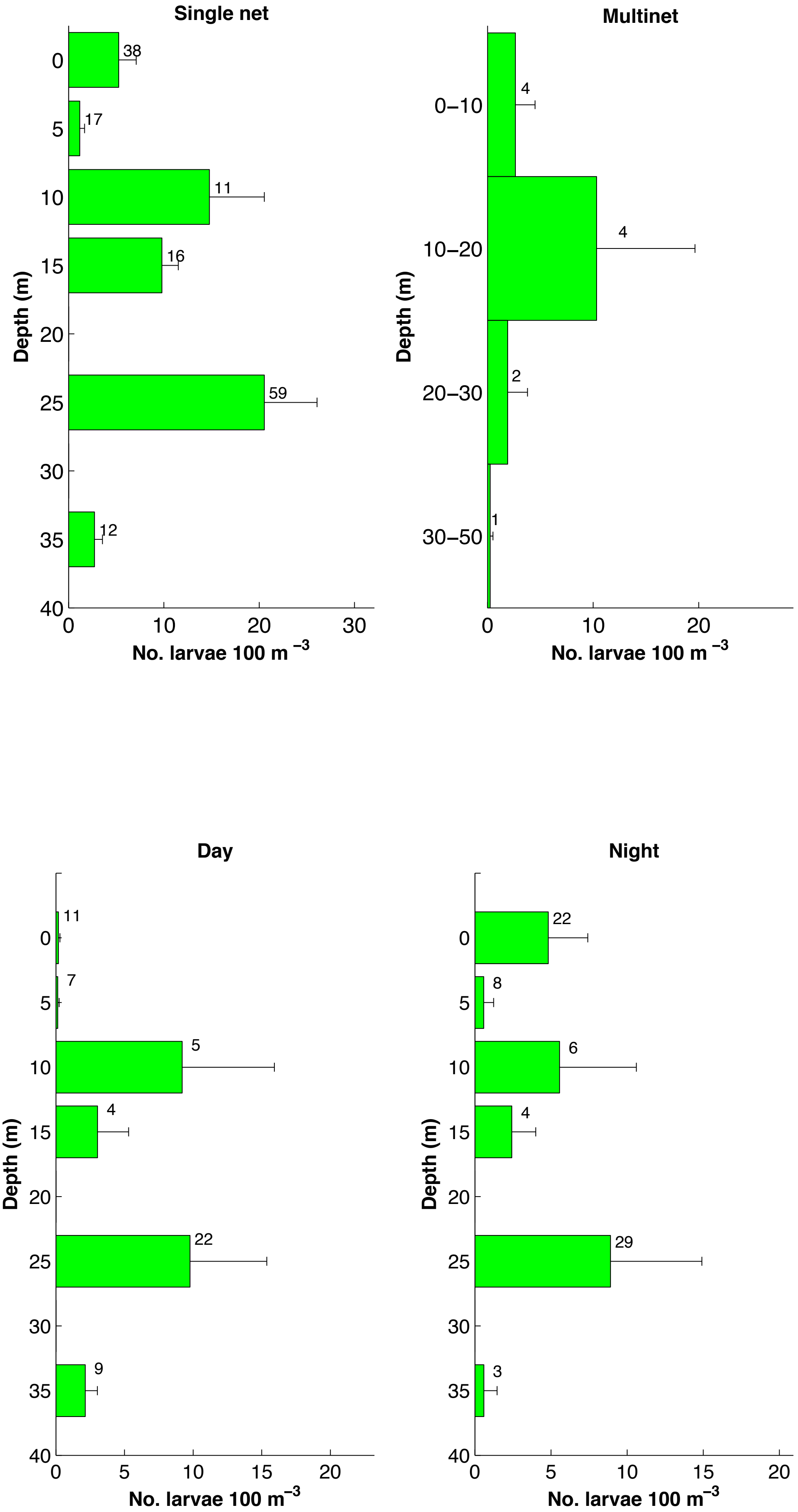
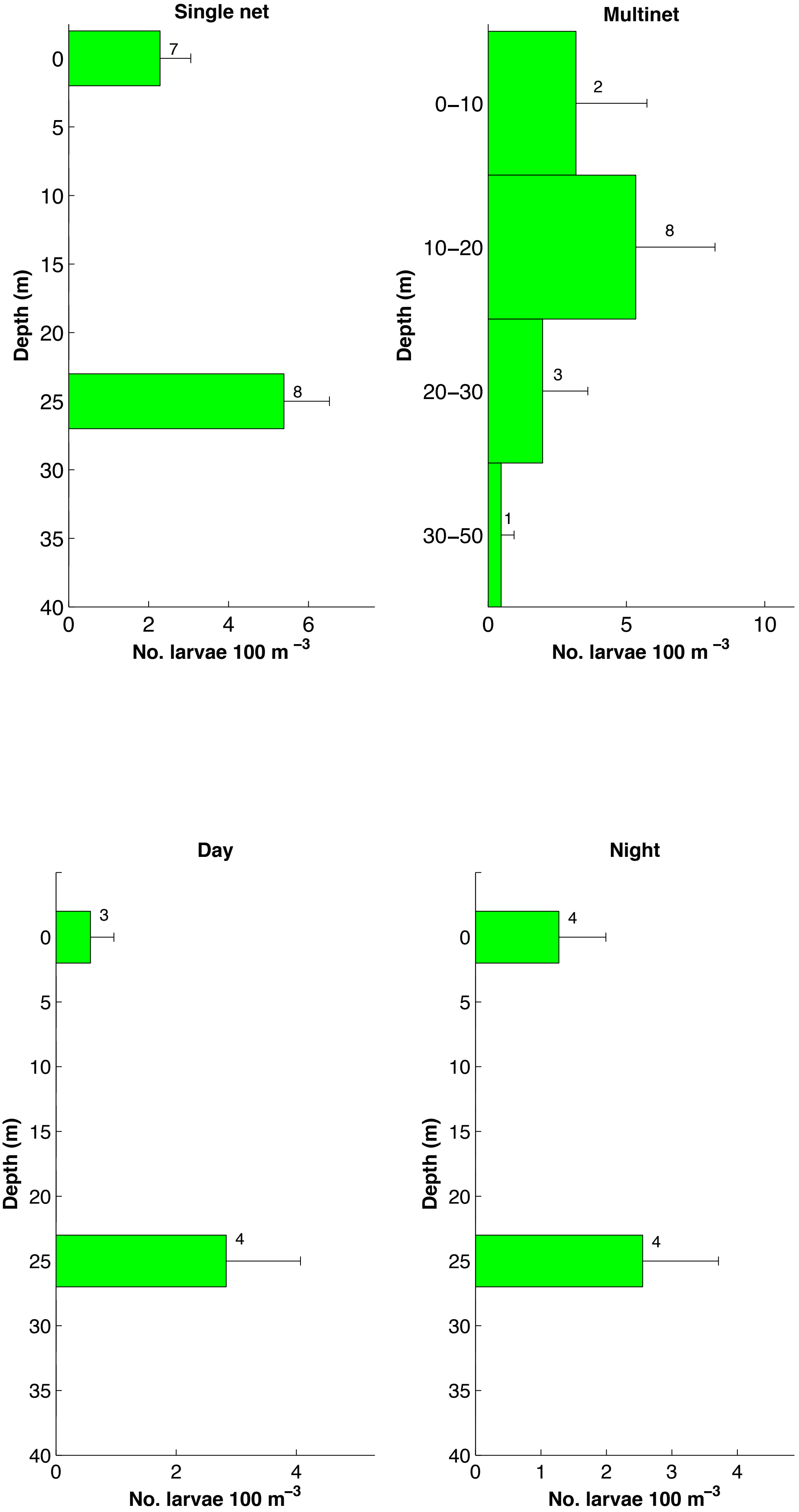
Carcinus maenas M



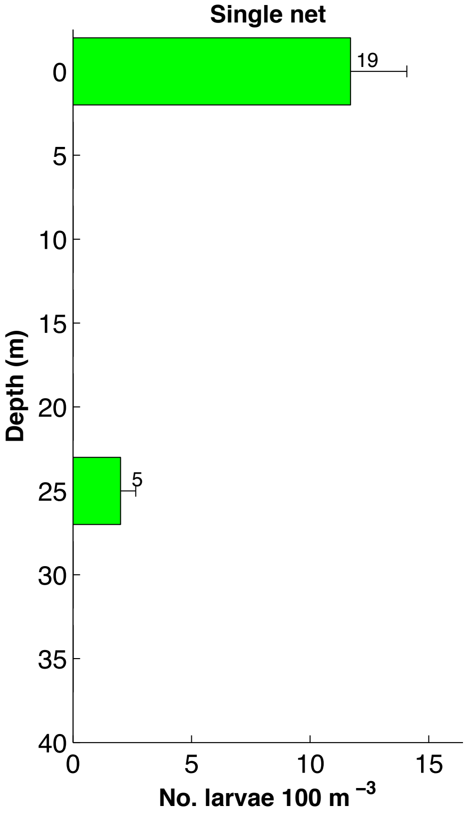
50

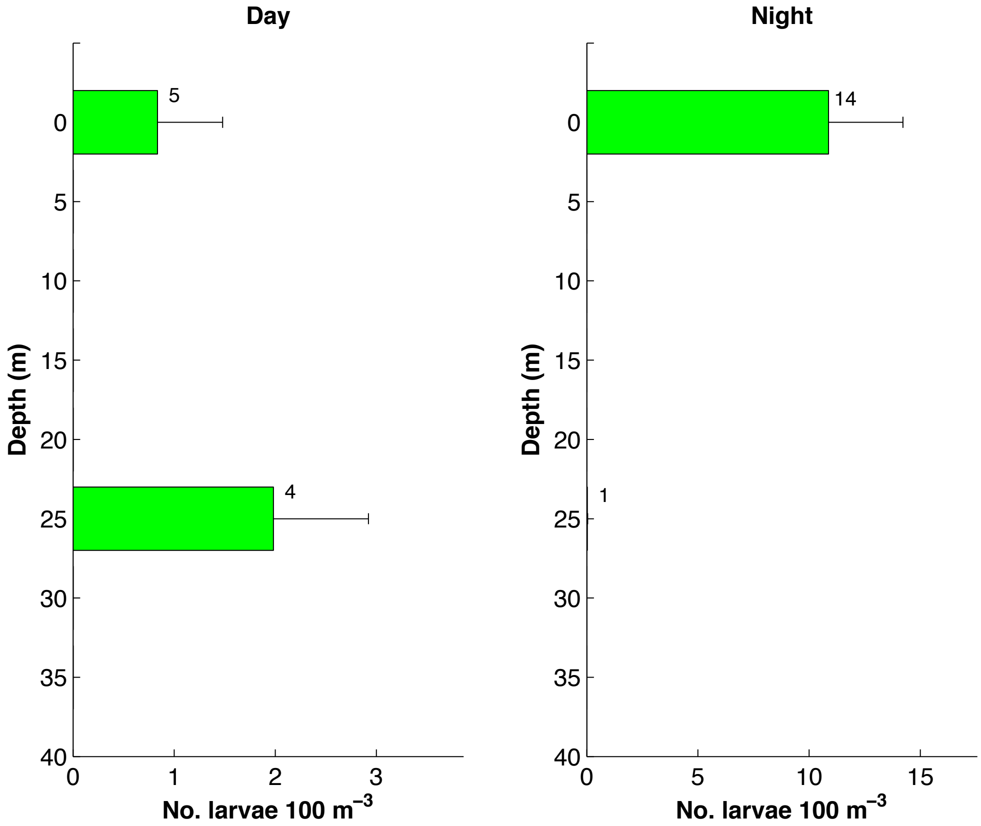
Liocarcinus navigator (cf.) Z1−2



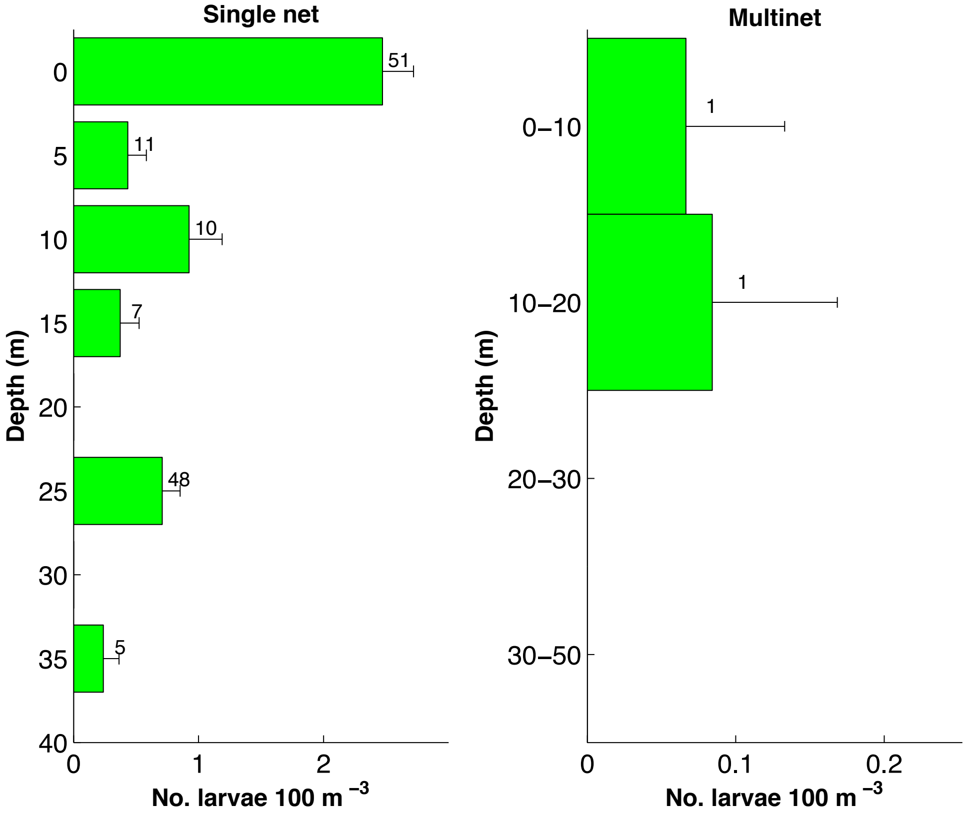
51

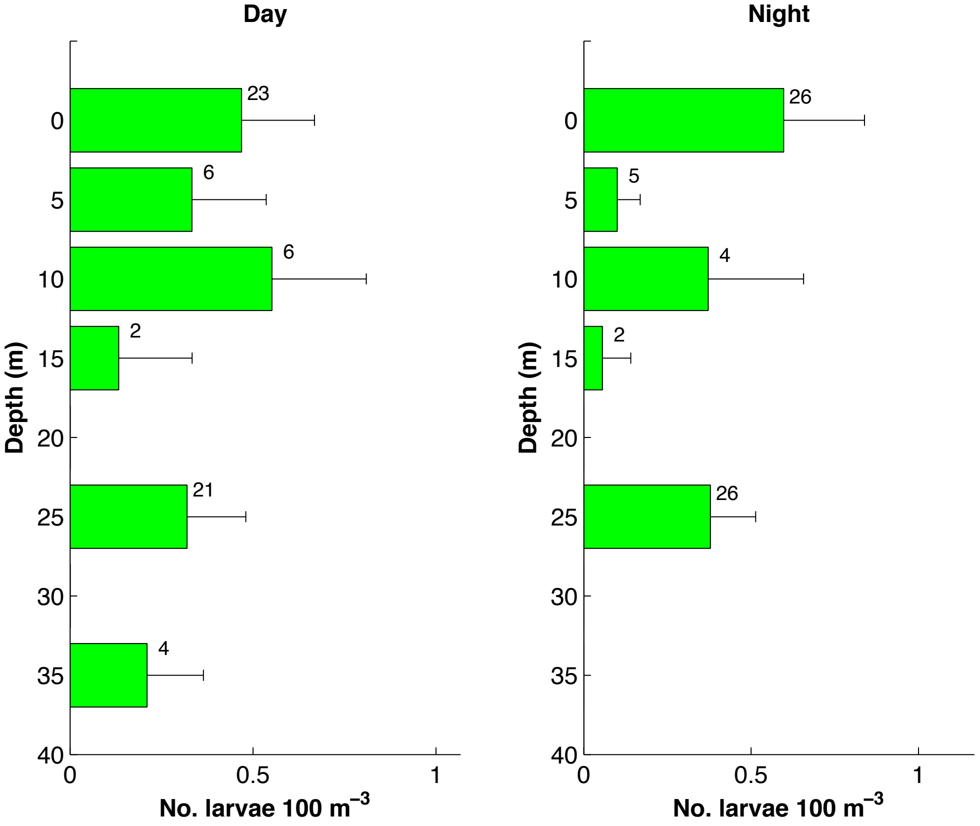
Liocarcinus navigator (cf.) Z3–5





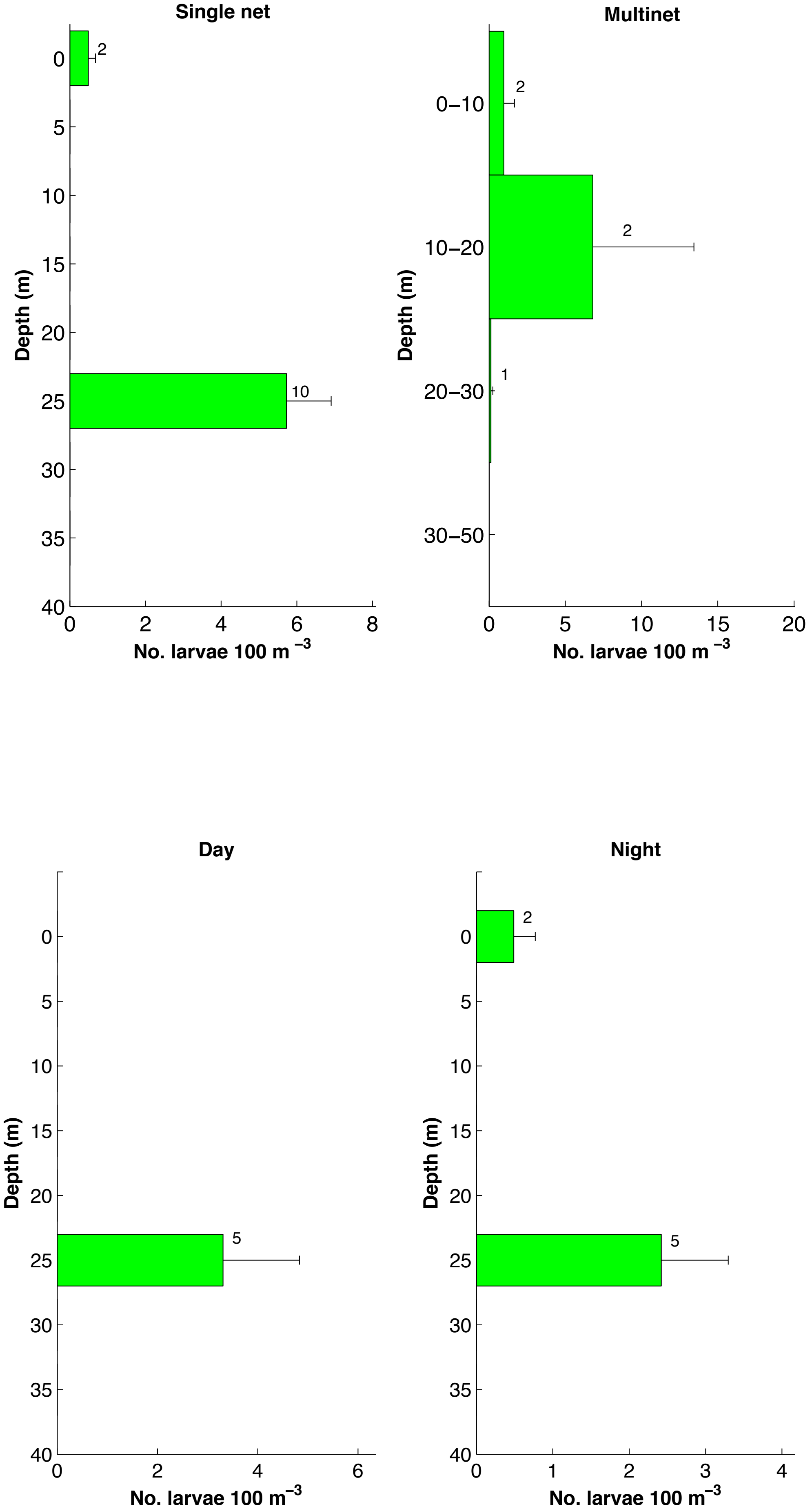
Liocarcinus navigator (cf.) M



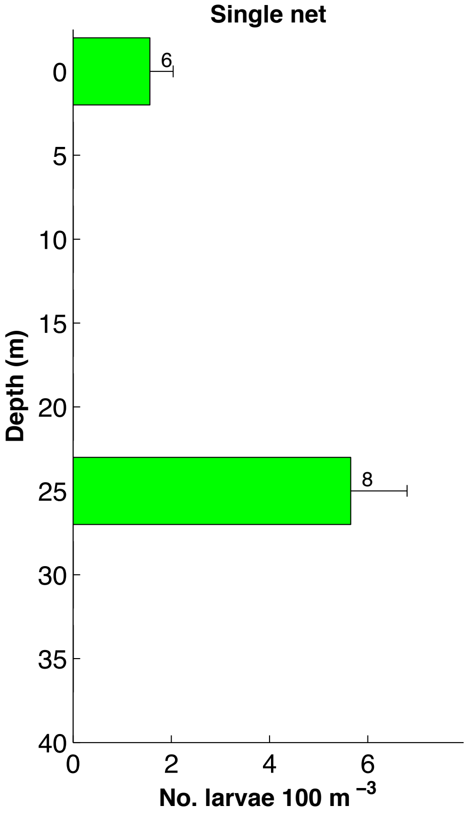


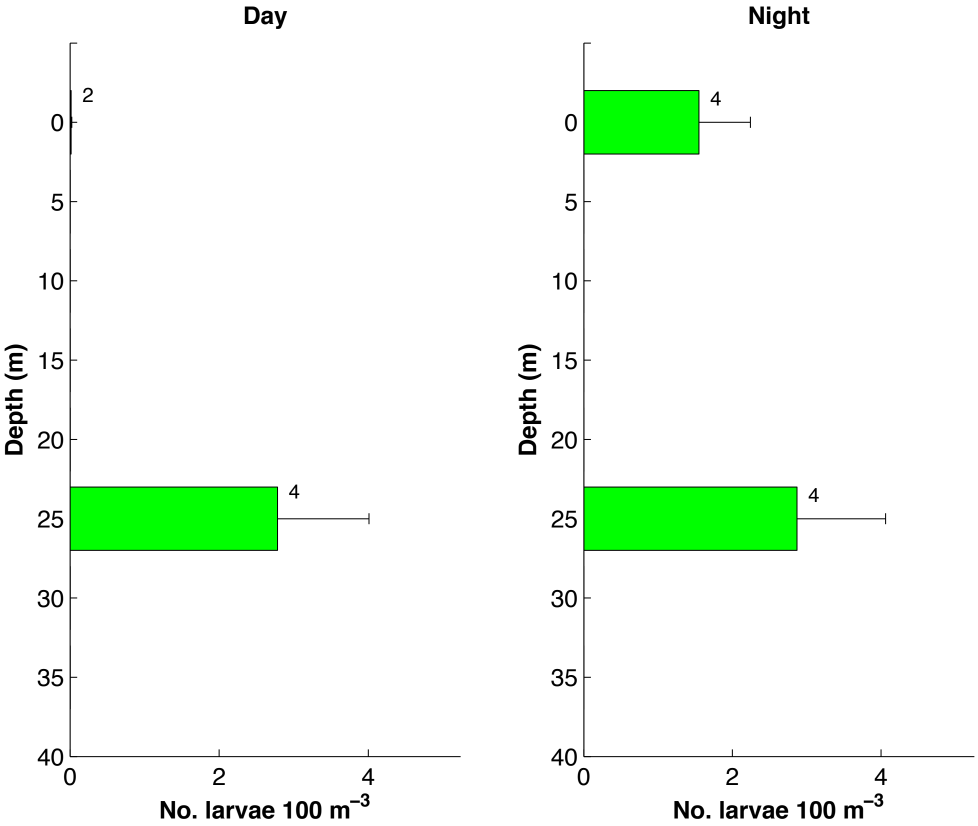
53

Liocarcinus depurator (cf.) Z1–2

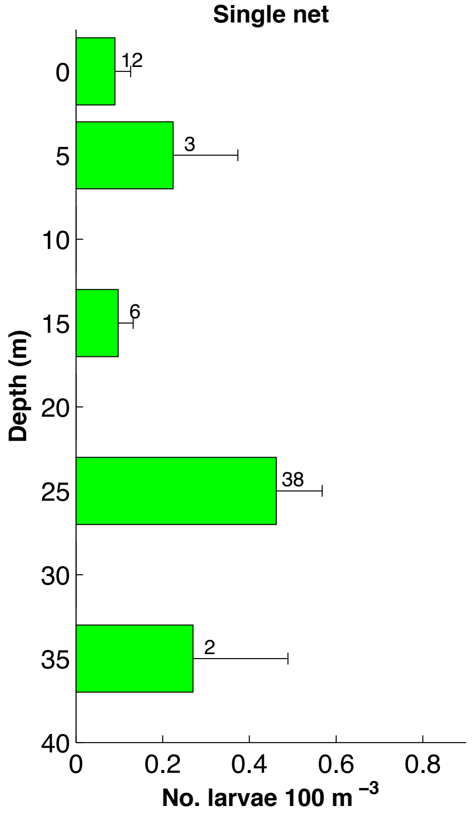


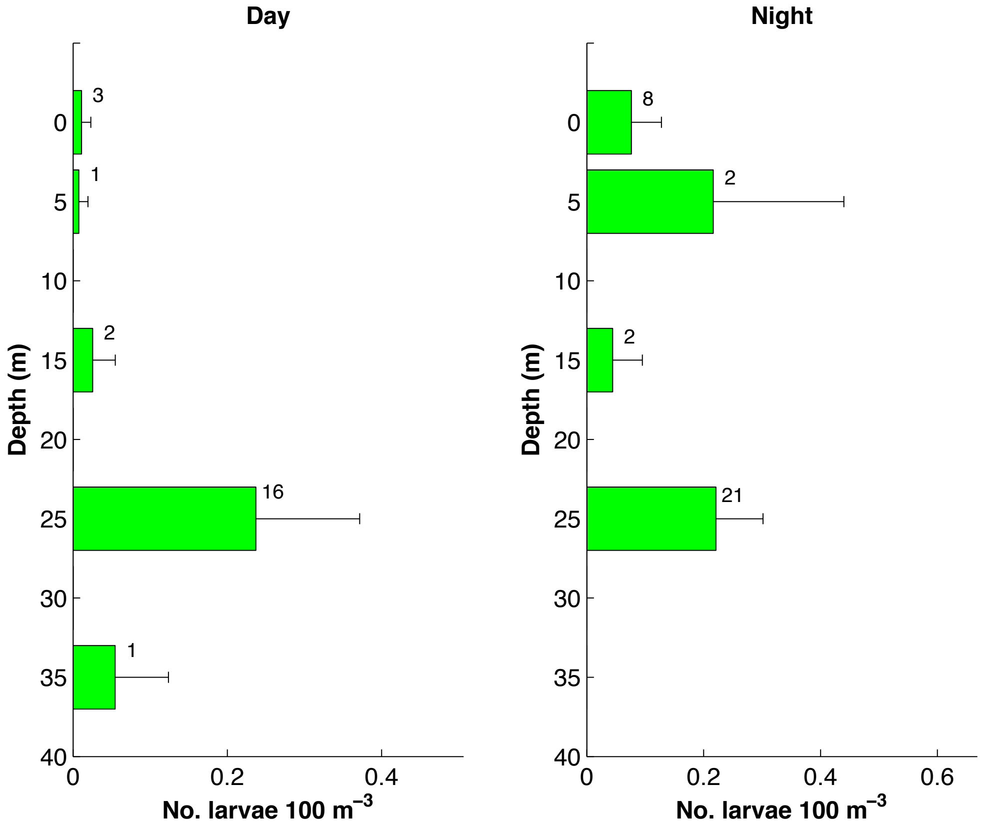
Liocarcinus depurator (cf.) Z3–5



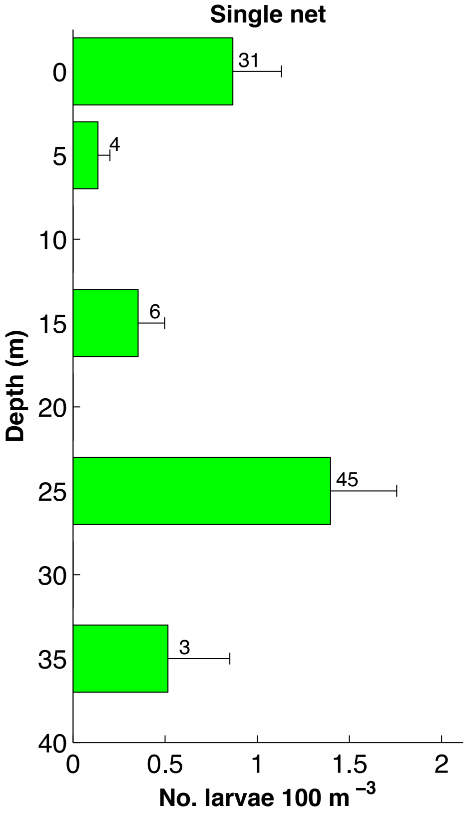


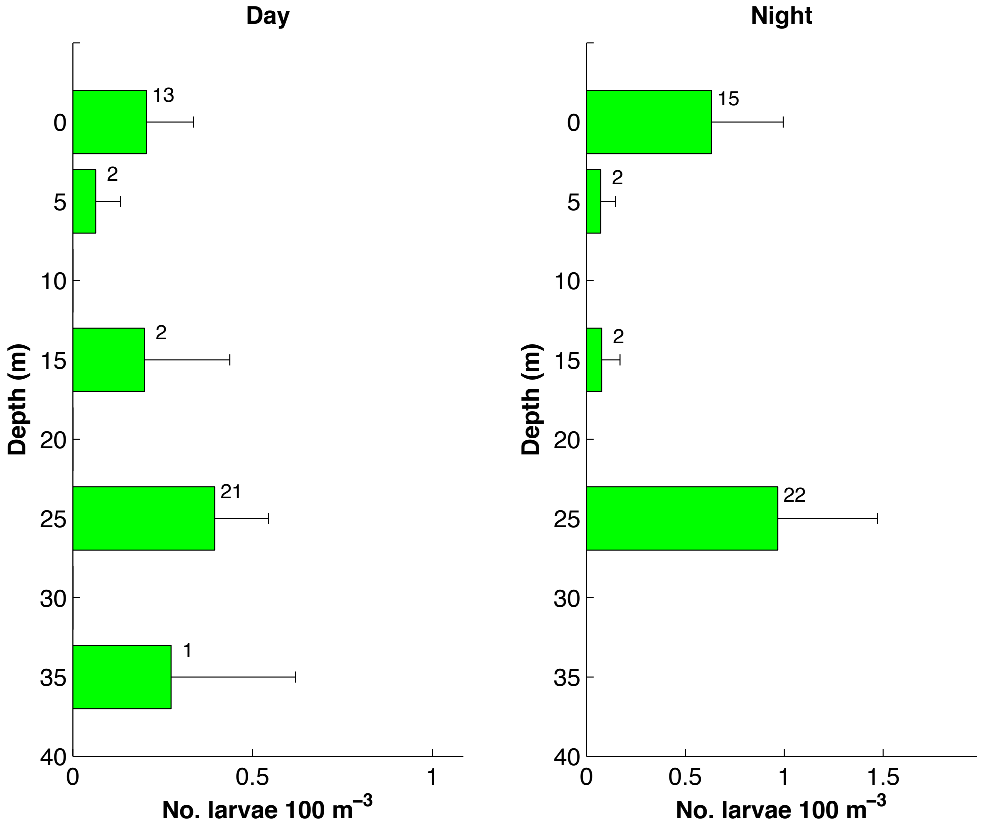
55 Liocarcinus depurator (cf.) M





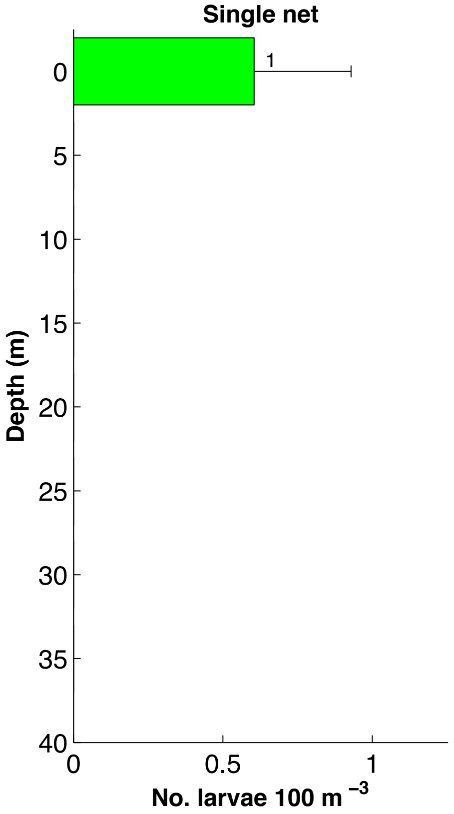
Liocarcinus sp. M

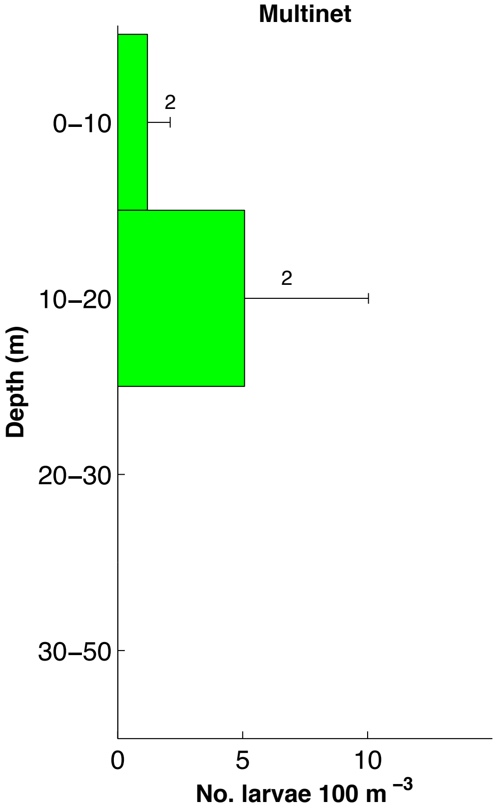


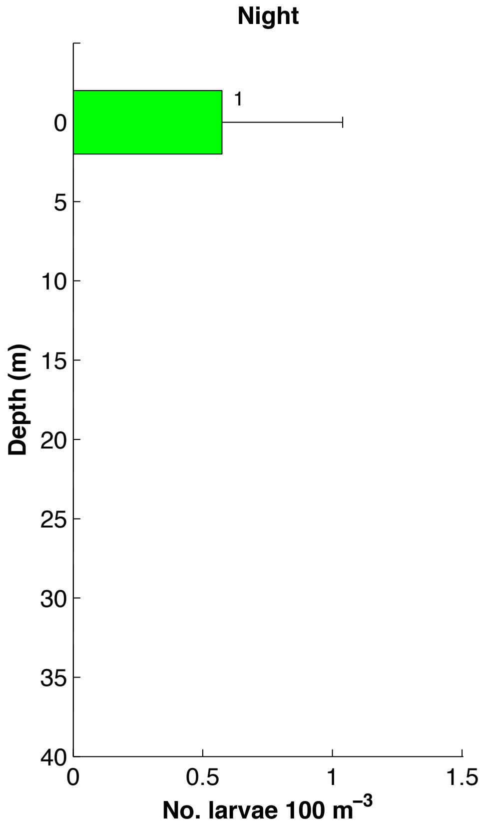


57

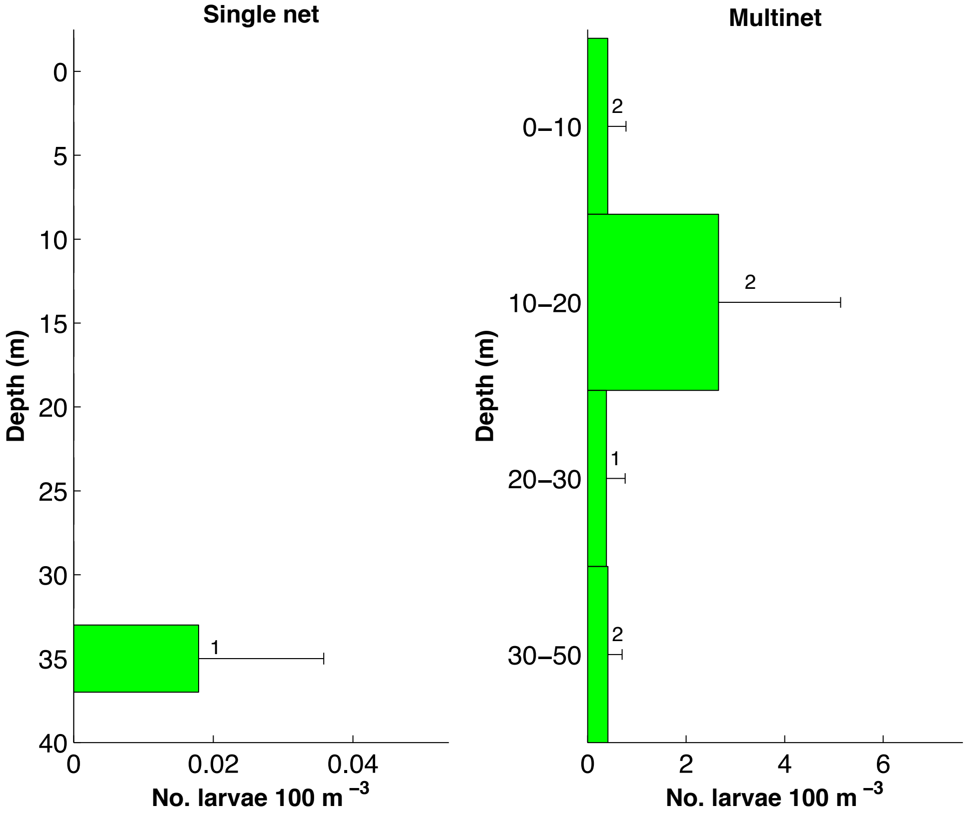
Necora puber (cf.) Z1–4

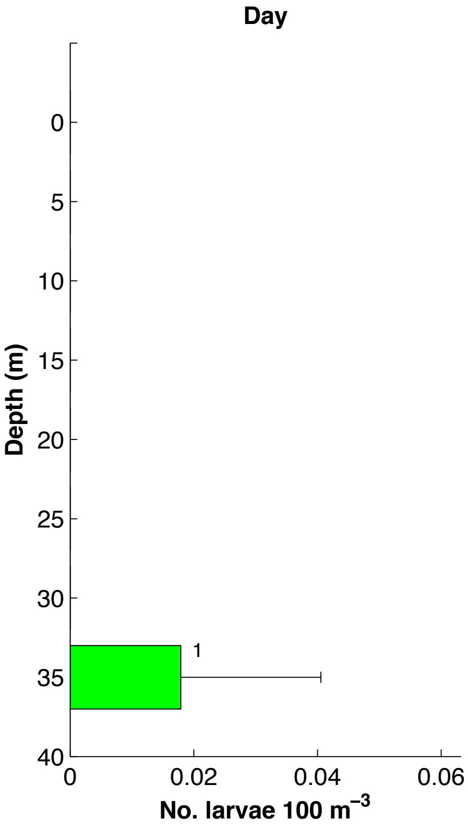






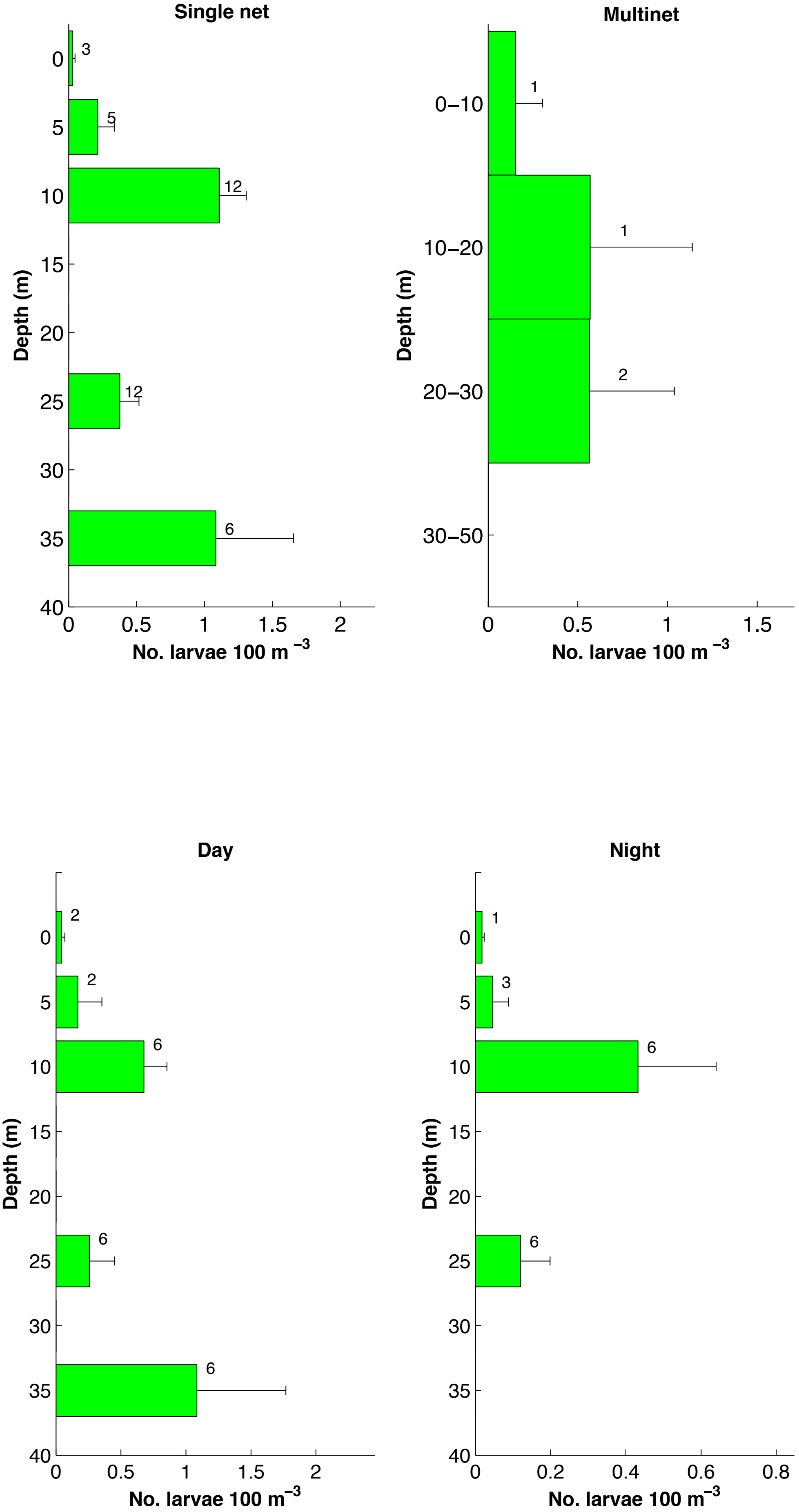
Necora puber (cf.) M





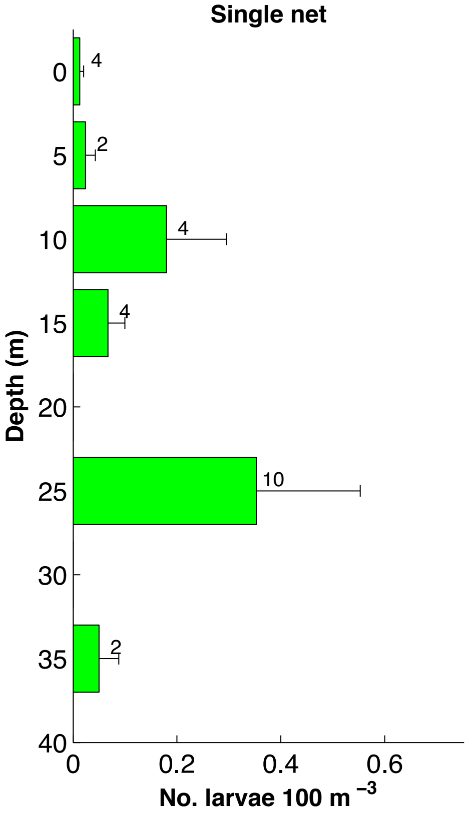
59

Portunid sp. M

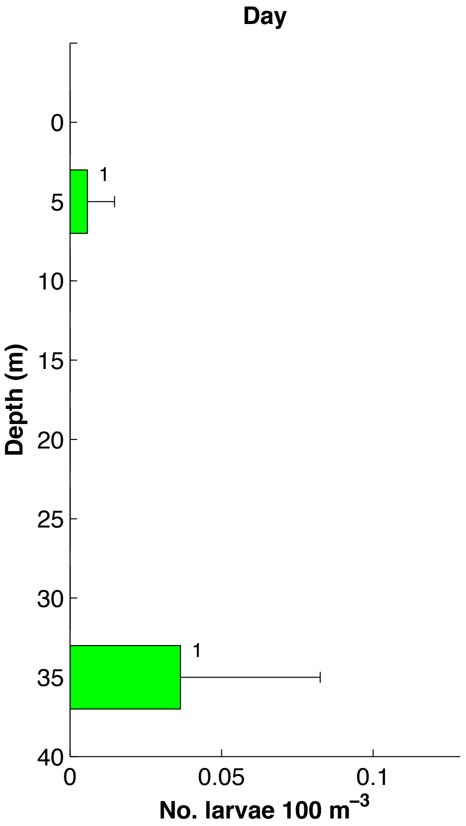


60

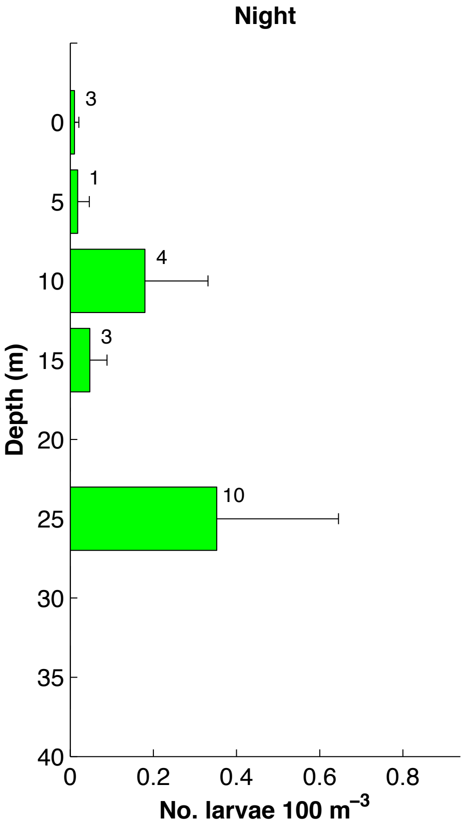
Portunid sp. Juvenile



Single net



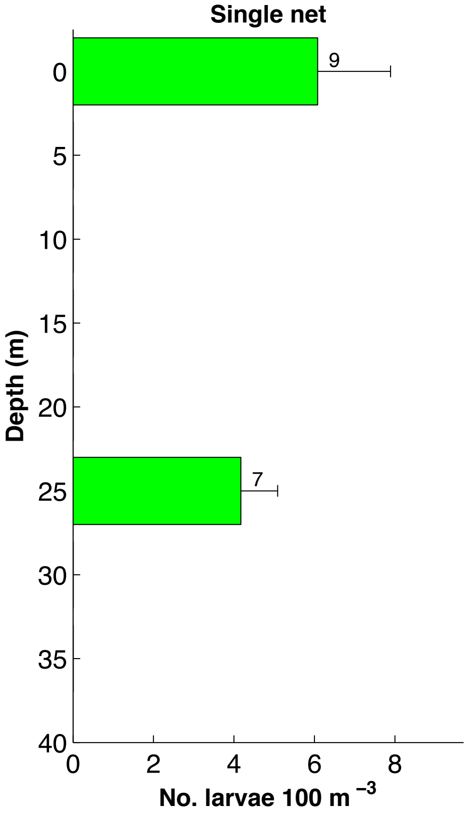
Day

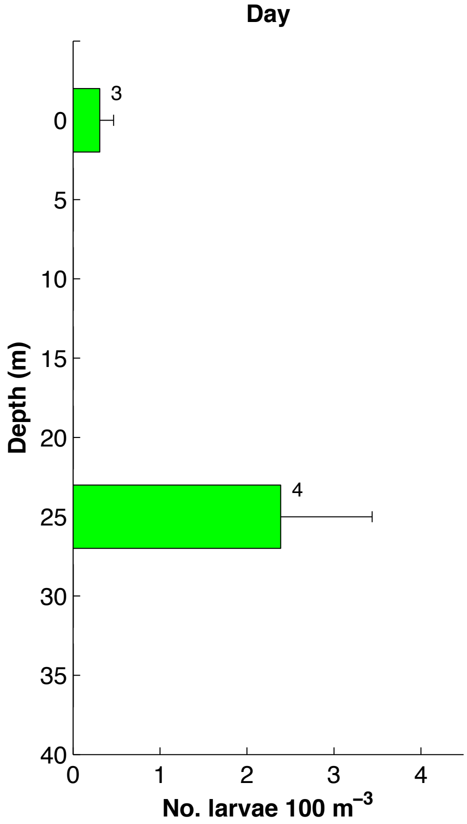


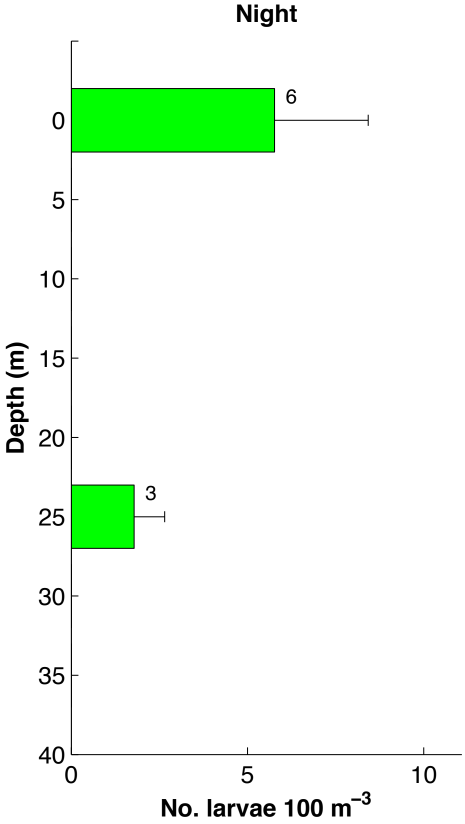
Night

61

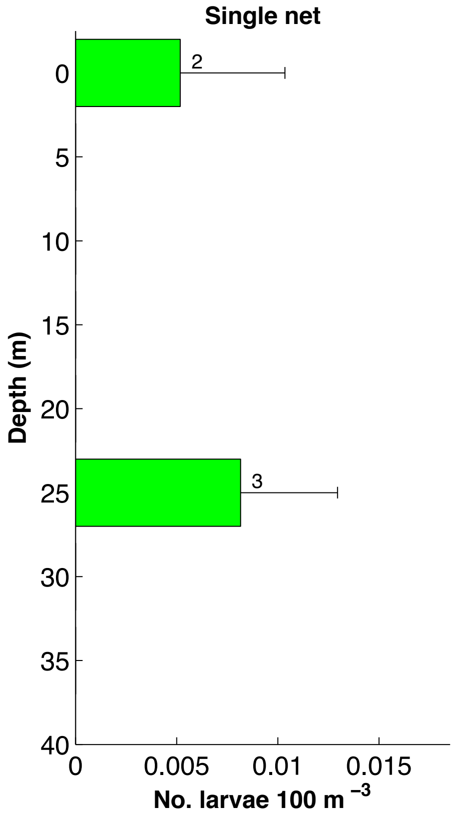
Pirimela denticulata (cf.) Z

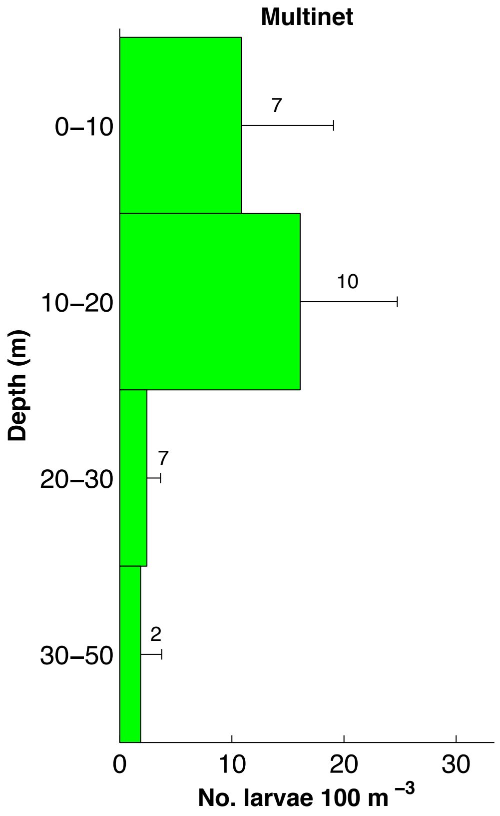


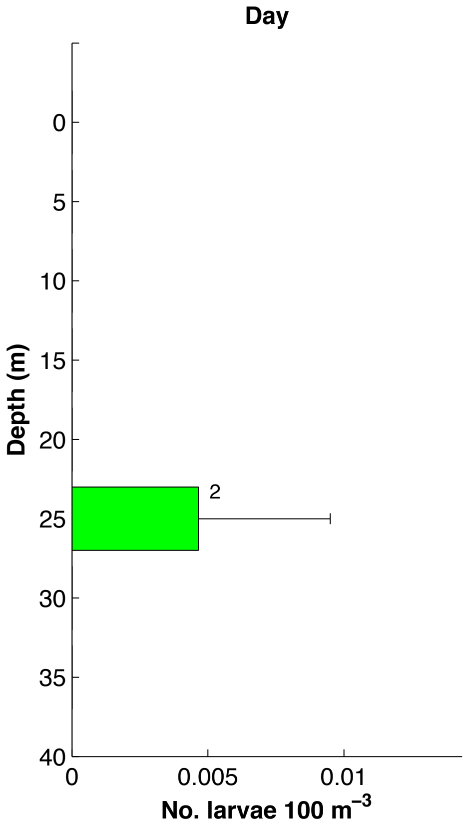


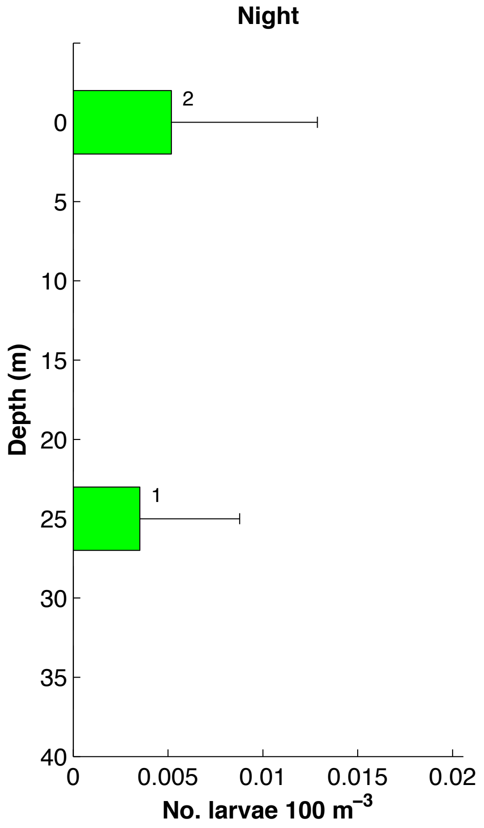


Cancer pagurus Z1–5





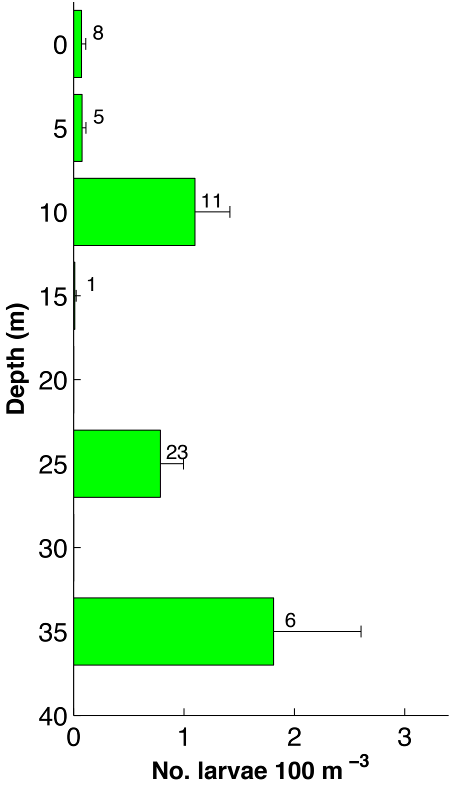




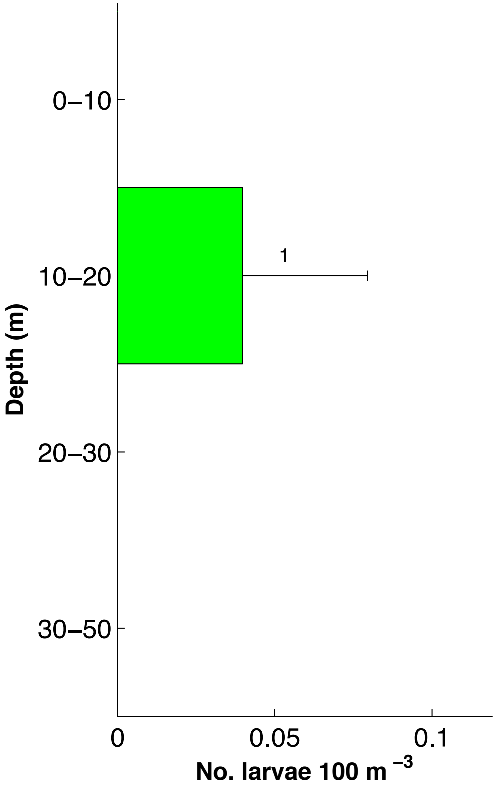
63

Cancer pagurus M

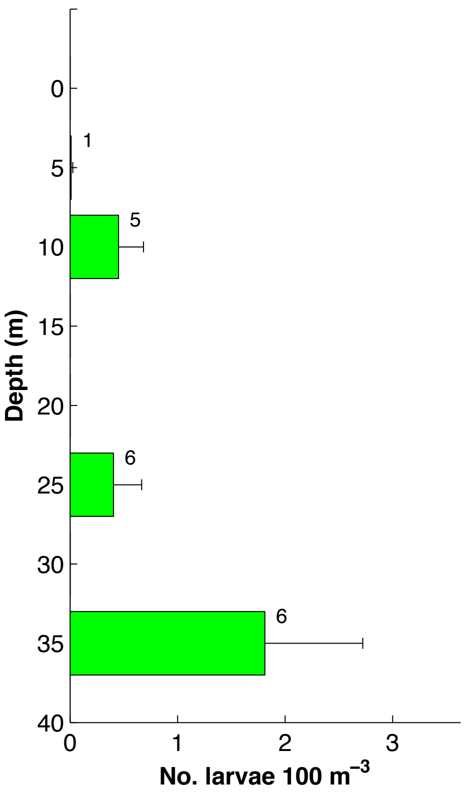
Single net



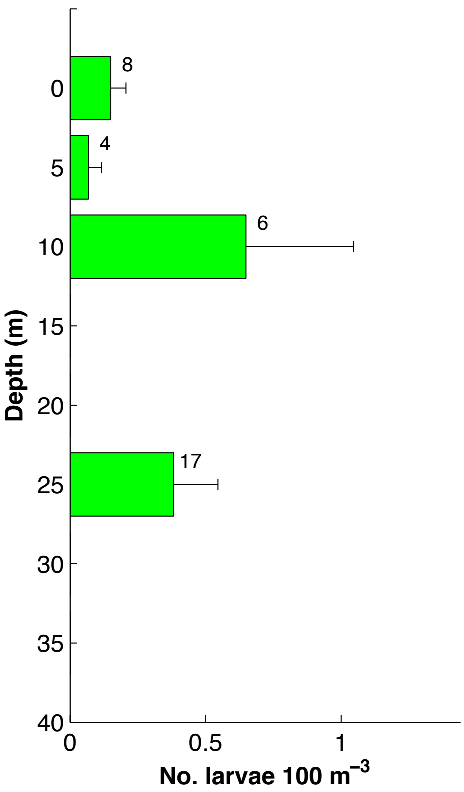
Multinet



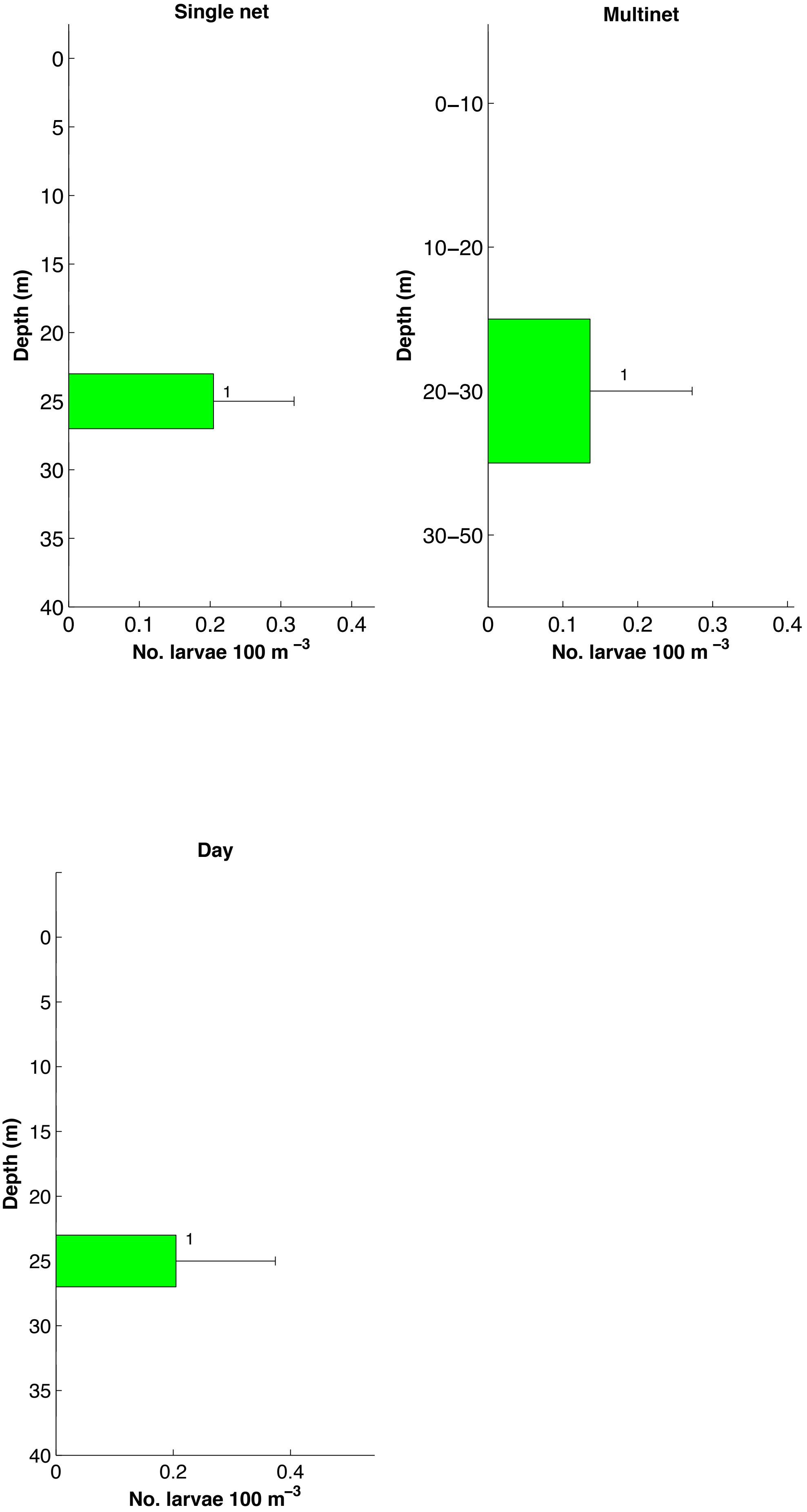
Day



Night

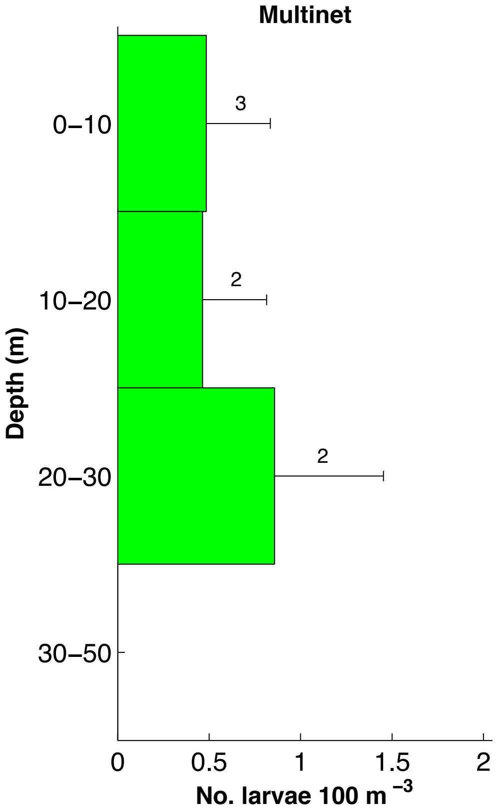


Thia scutella (cf.) Z1–3

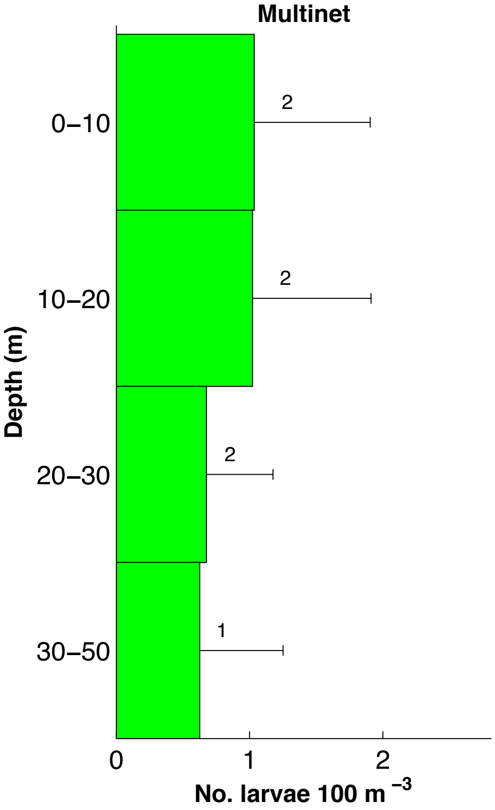


65

Corystes cassivelaunus Z1–3

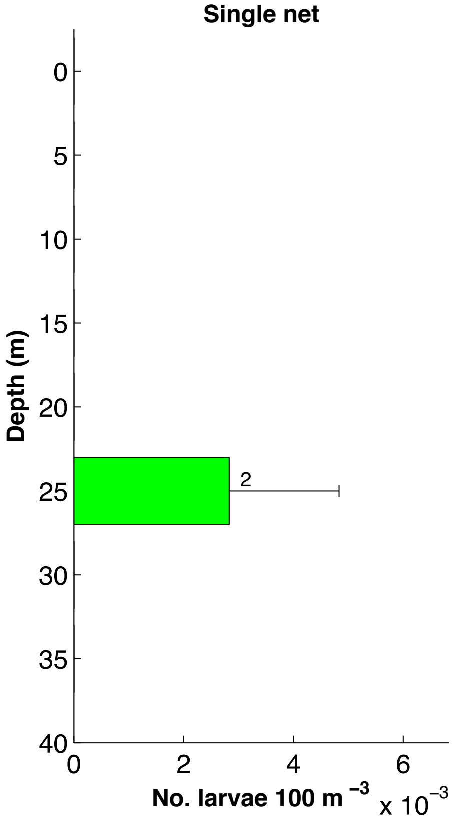


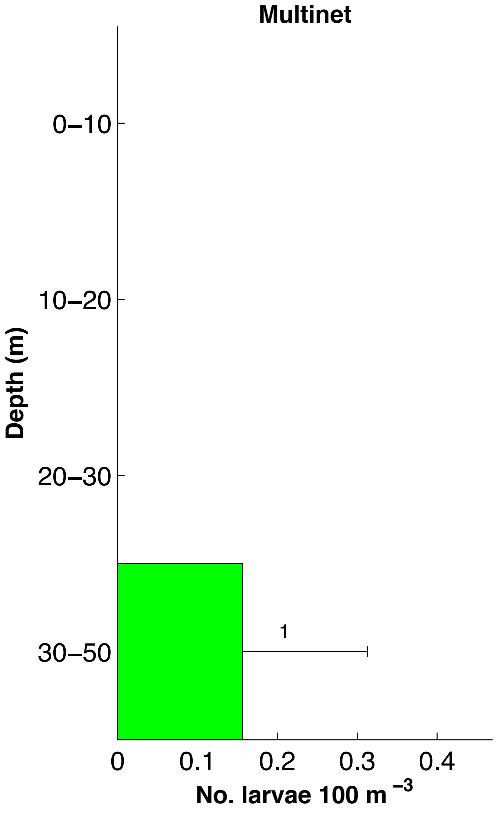
Corystes cassivelaunus Z4–5

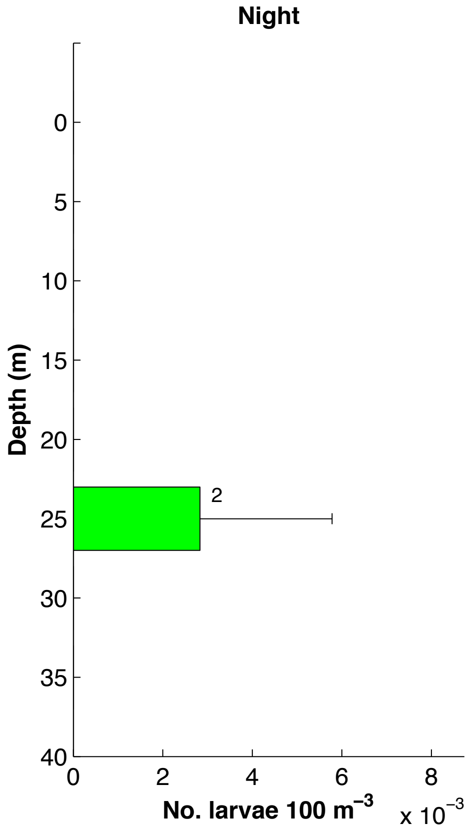


67

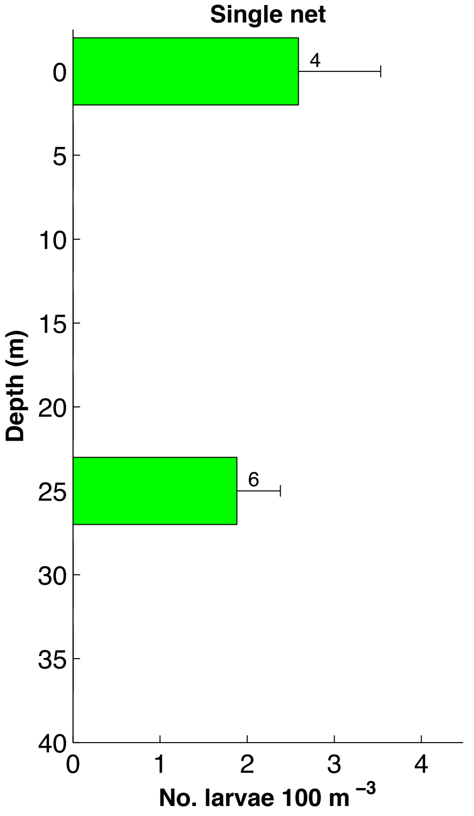
Corystes cassivelaunus M

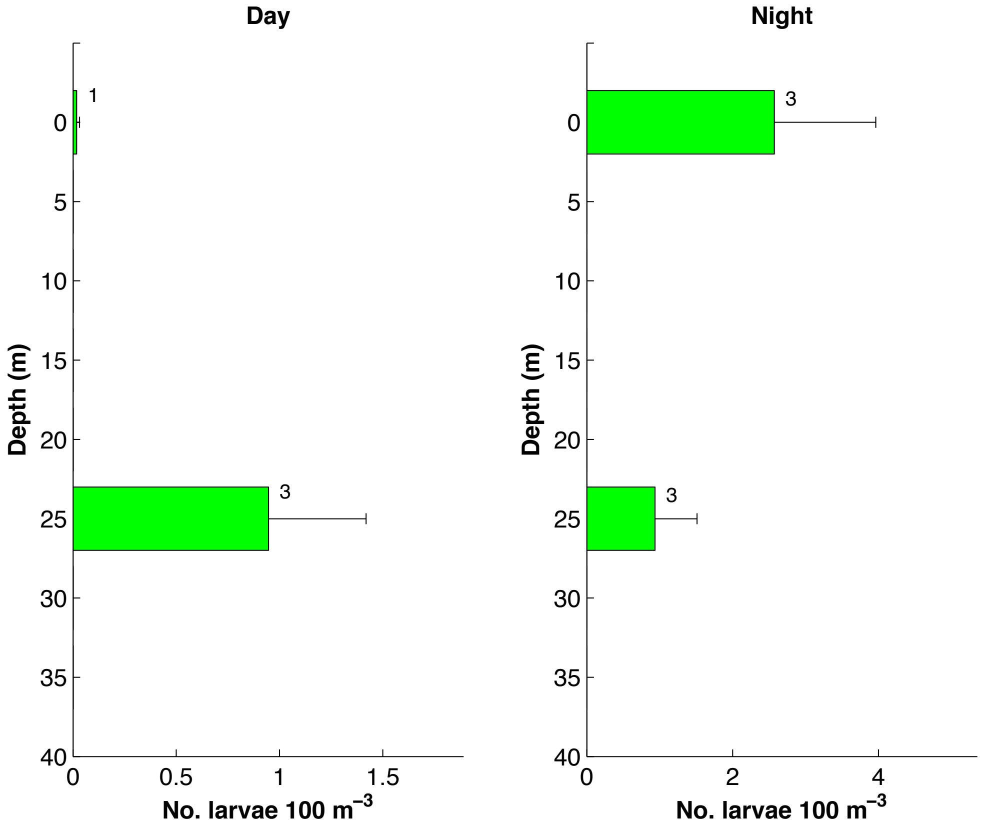






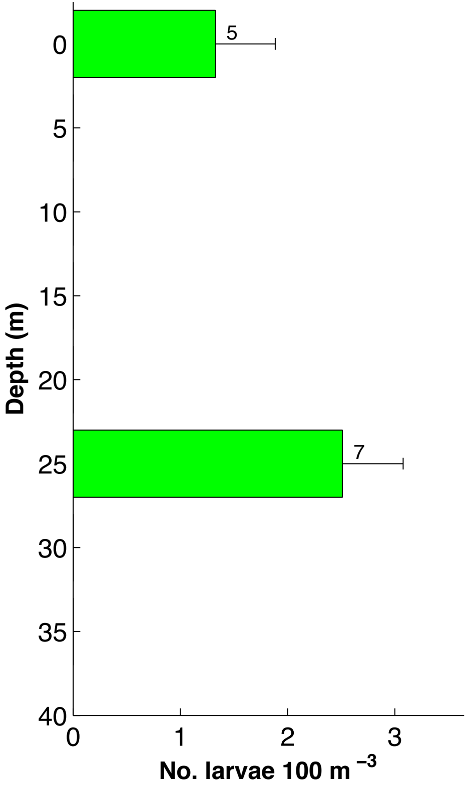
Atelecyclus rotundatus Z1−3



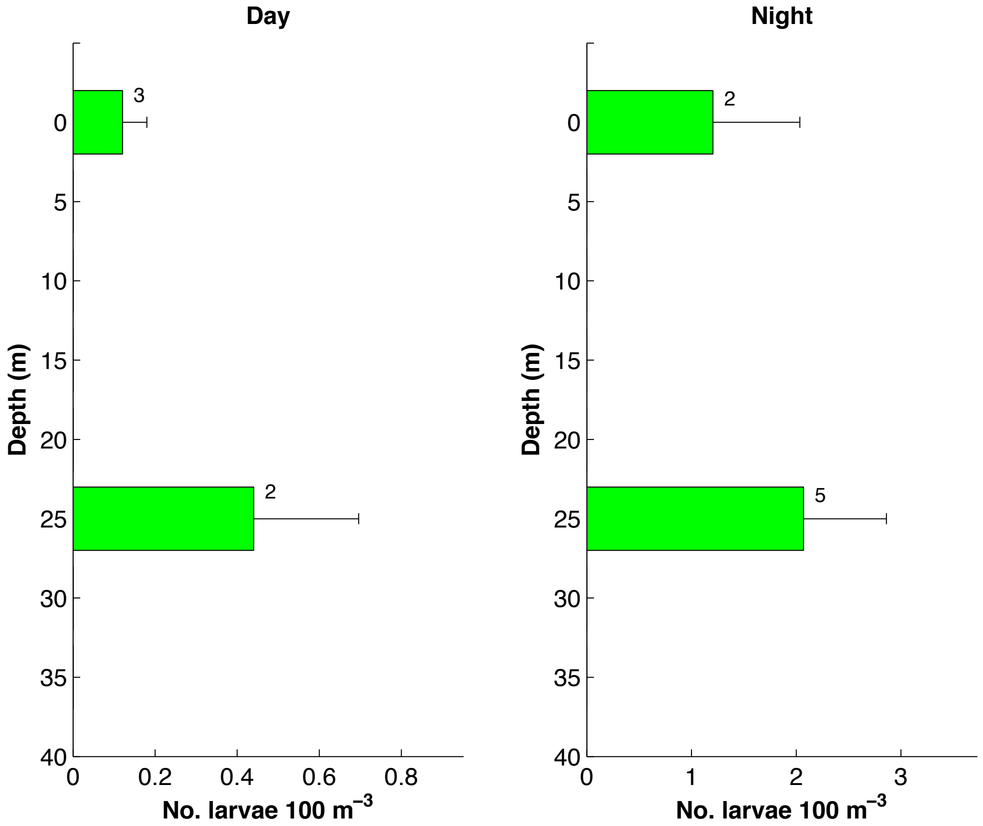


69

Atelecyclus rotundatus Z4–5



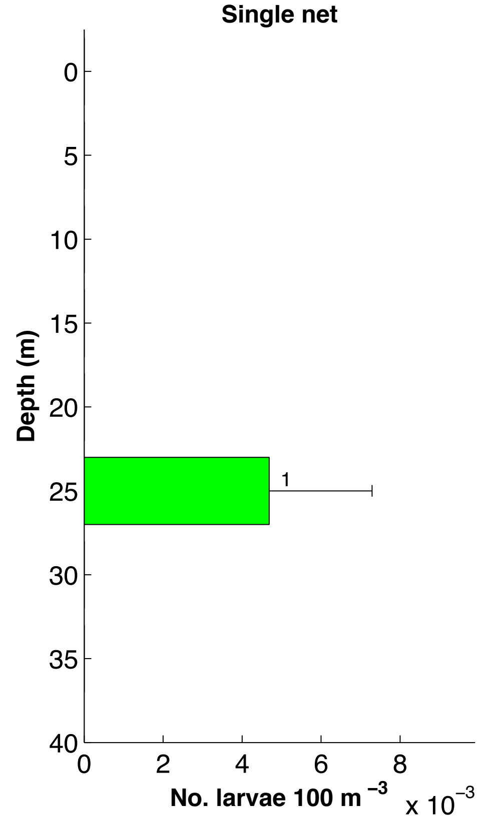
Single net

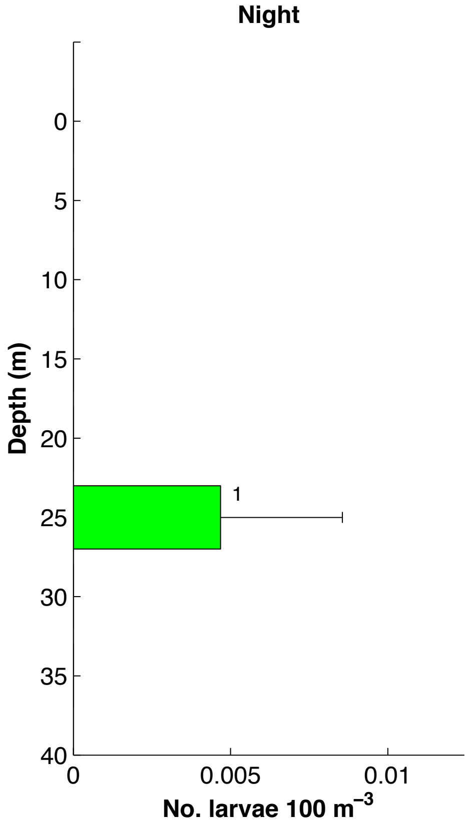


Day

Night

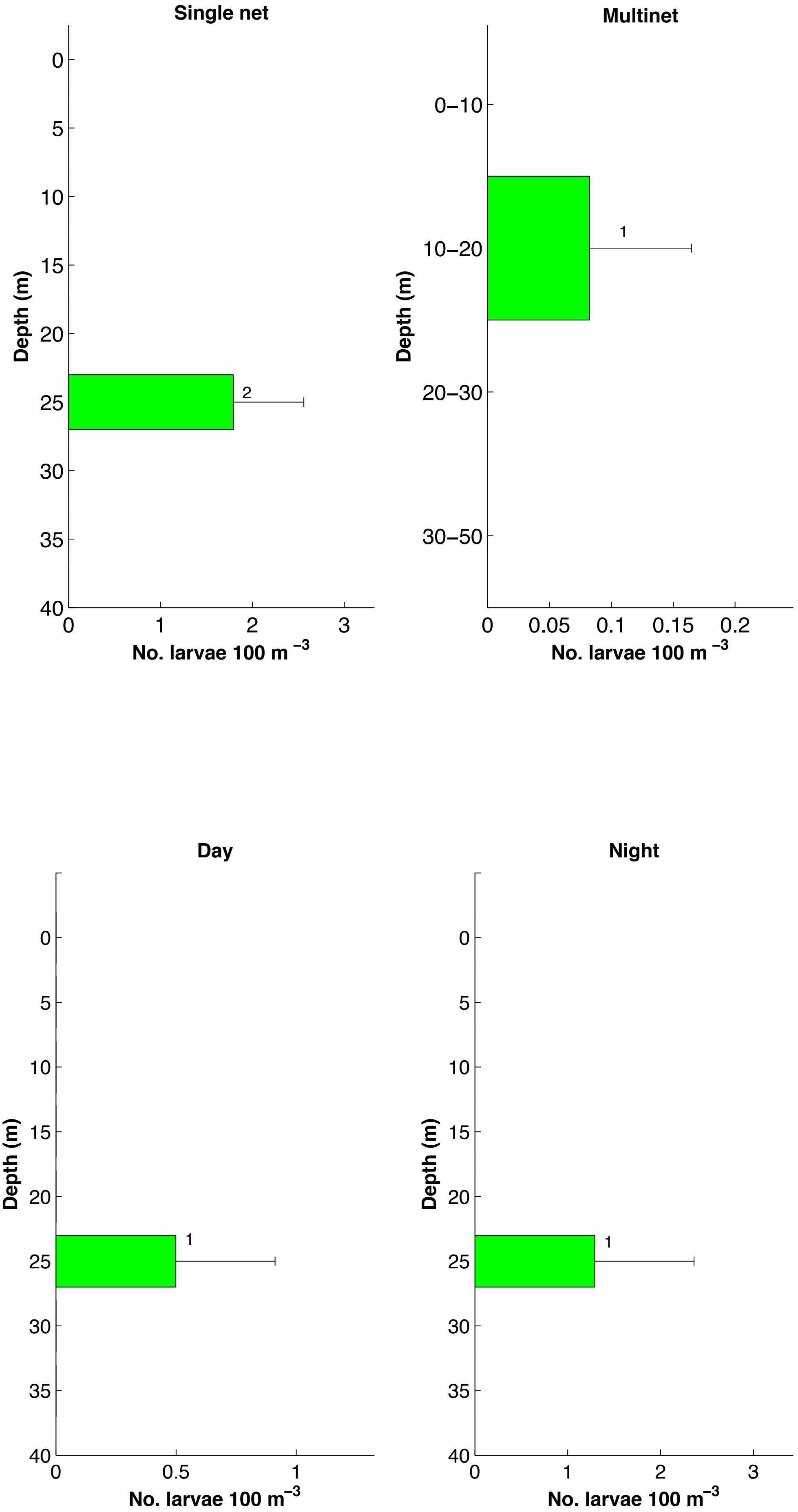
Atelecyclus rotundatus M



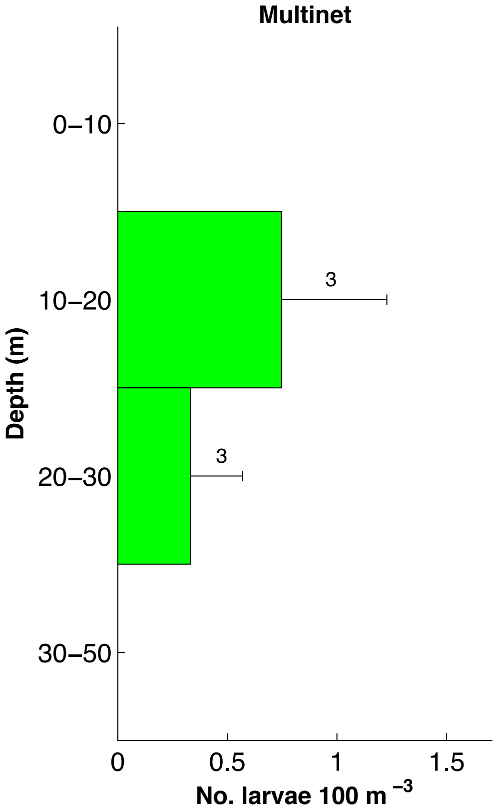


71

Hyas spp. Z1–2

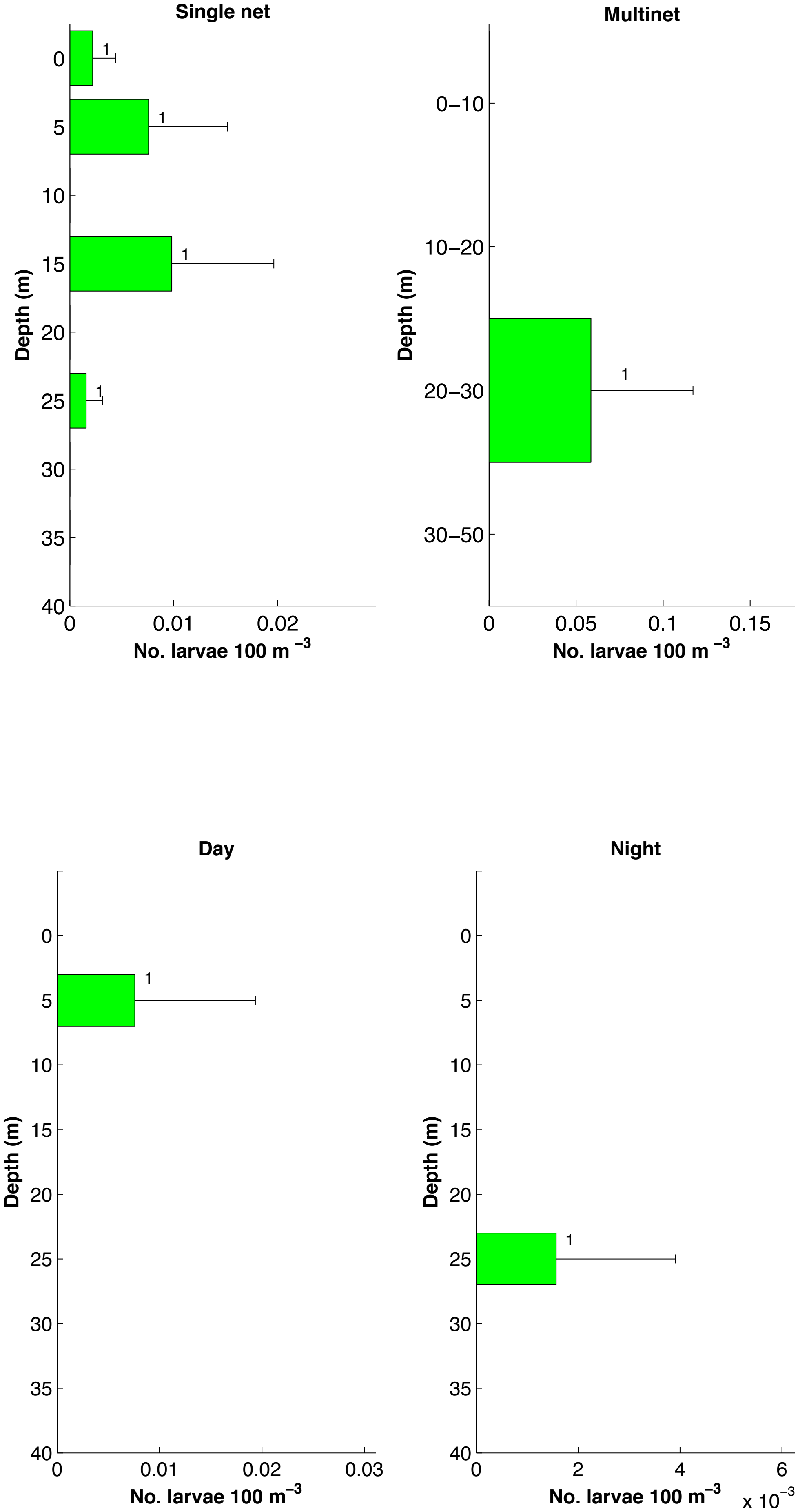


Hyas spp. M

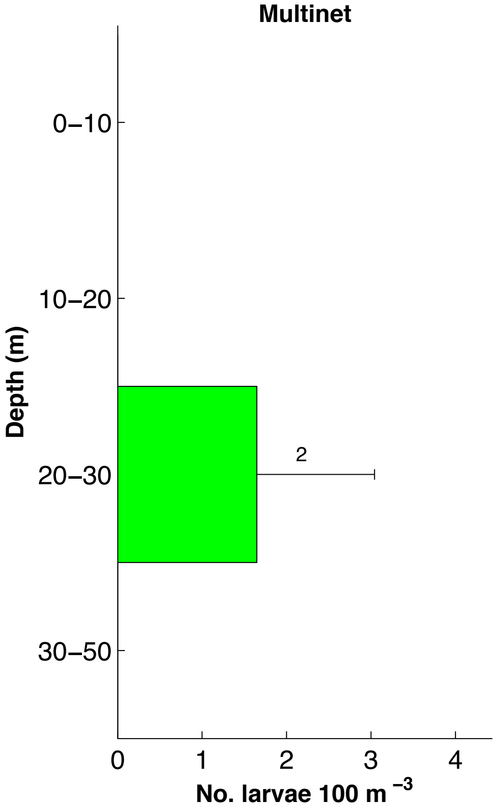

Multinet
Depth (m)
0–10
10–20
20–30
30–50
3
3
0
0.5
1
1.5
No. larvae 100 m $^{-3}$

73

Macropodia rostrata M



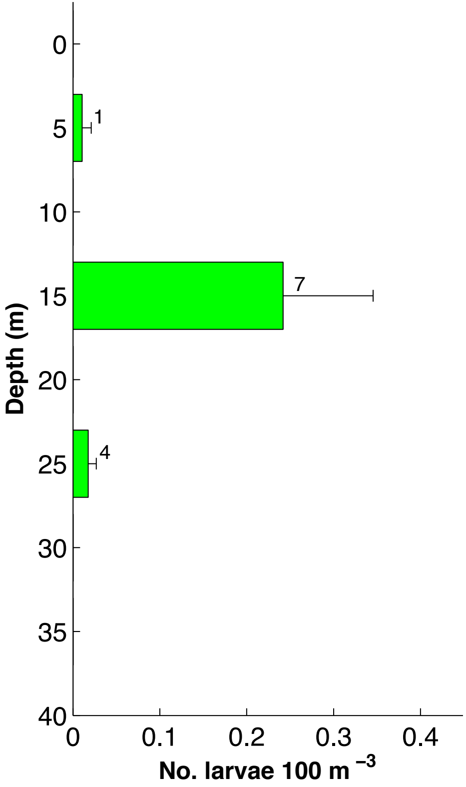
Euronyme spp. (cf.) Z1–2



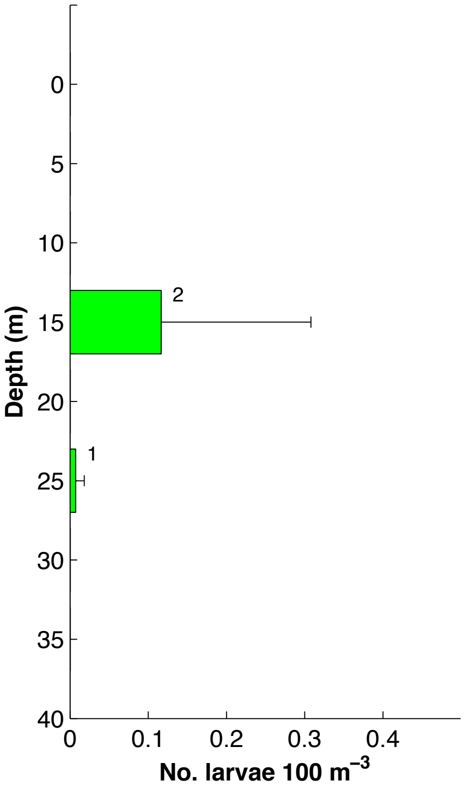
75

Euronyme spp. (cf.) M

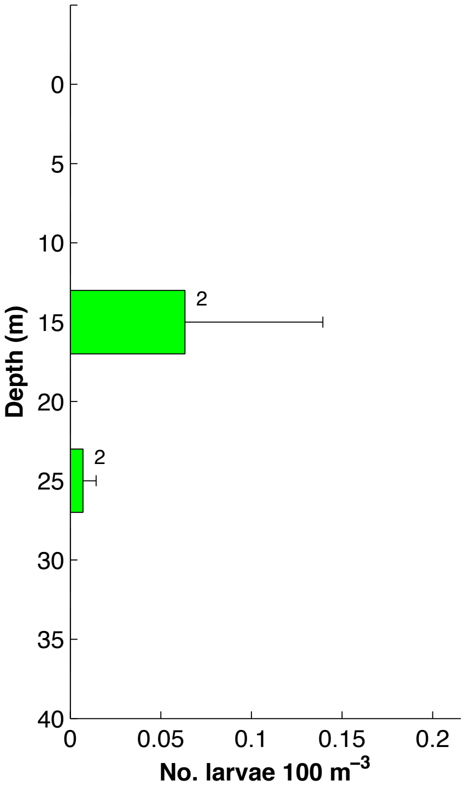
Single net



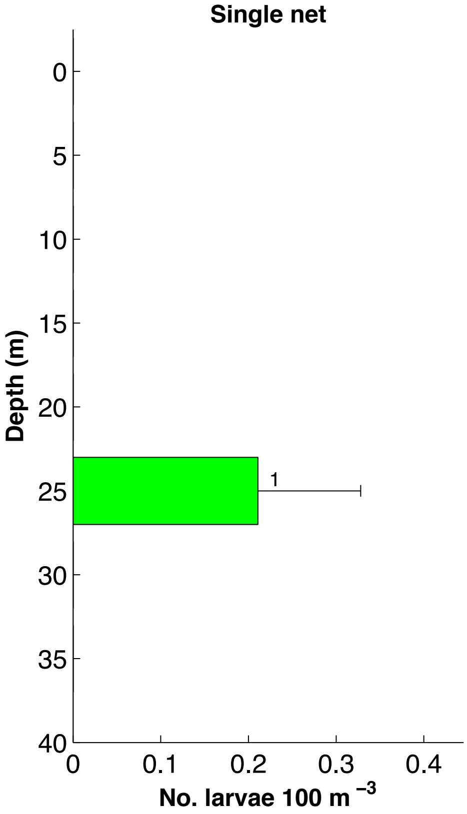
Day

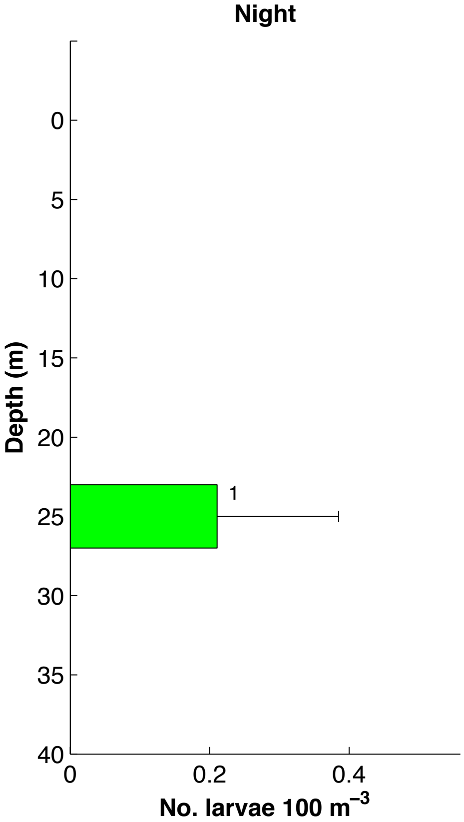


Night



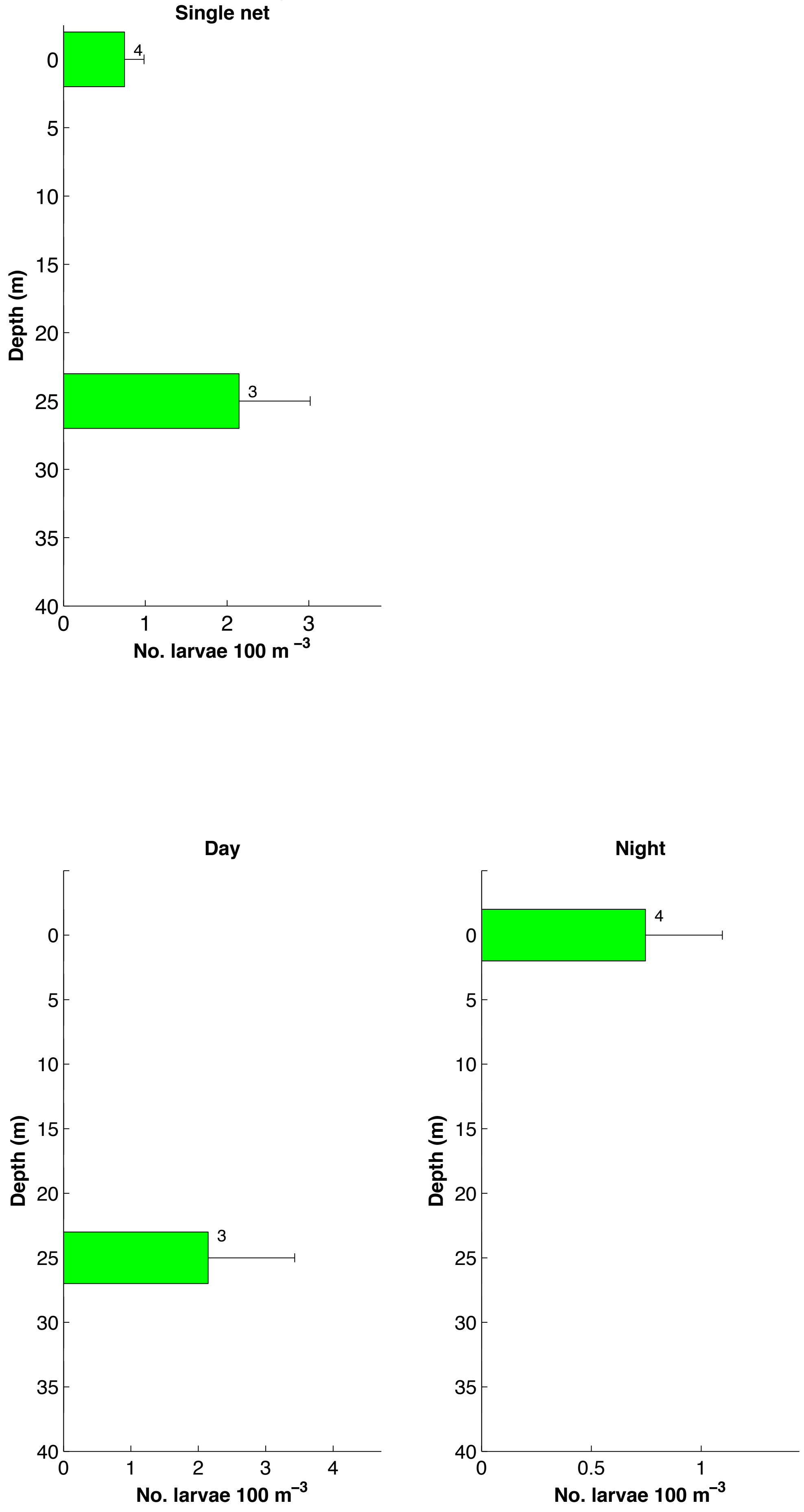
Pinnotheres pisum (cf.) Z



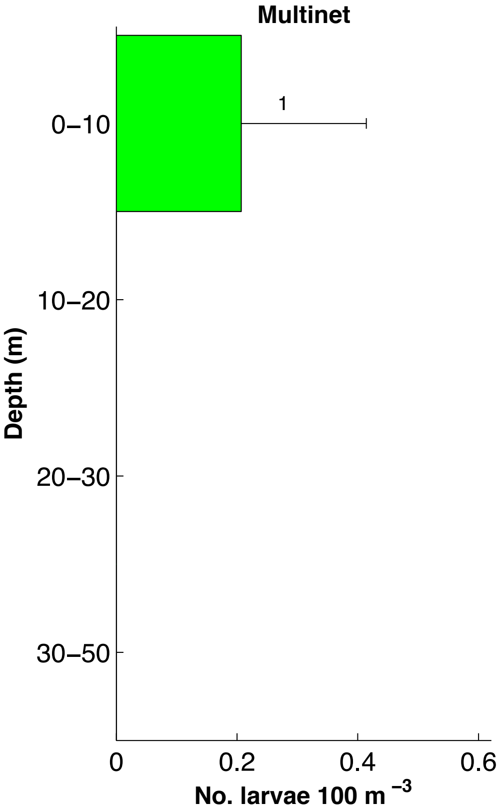


77

Geryon trispinosus (cf.) Z1–3

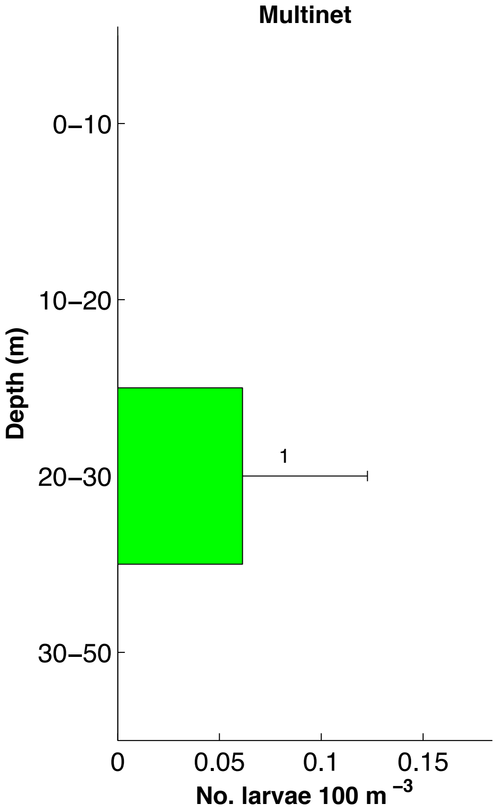


Pilumnus hurtellus (cf.) Z1

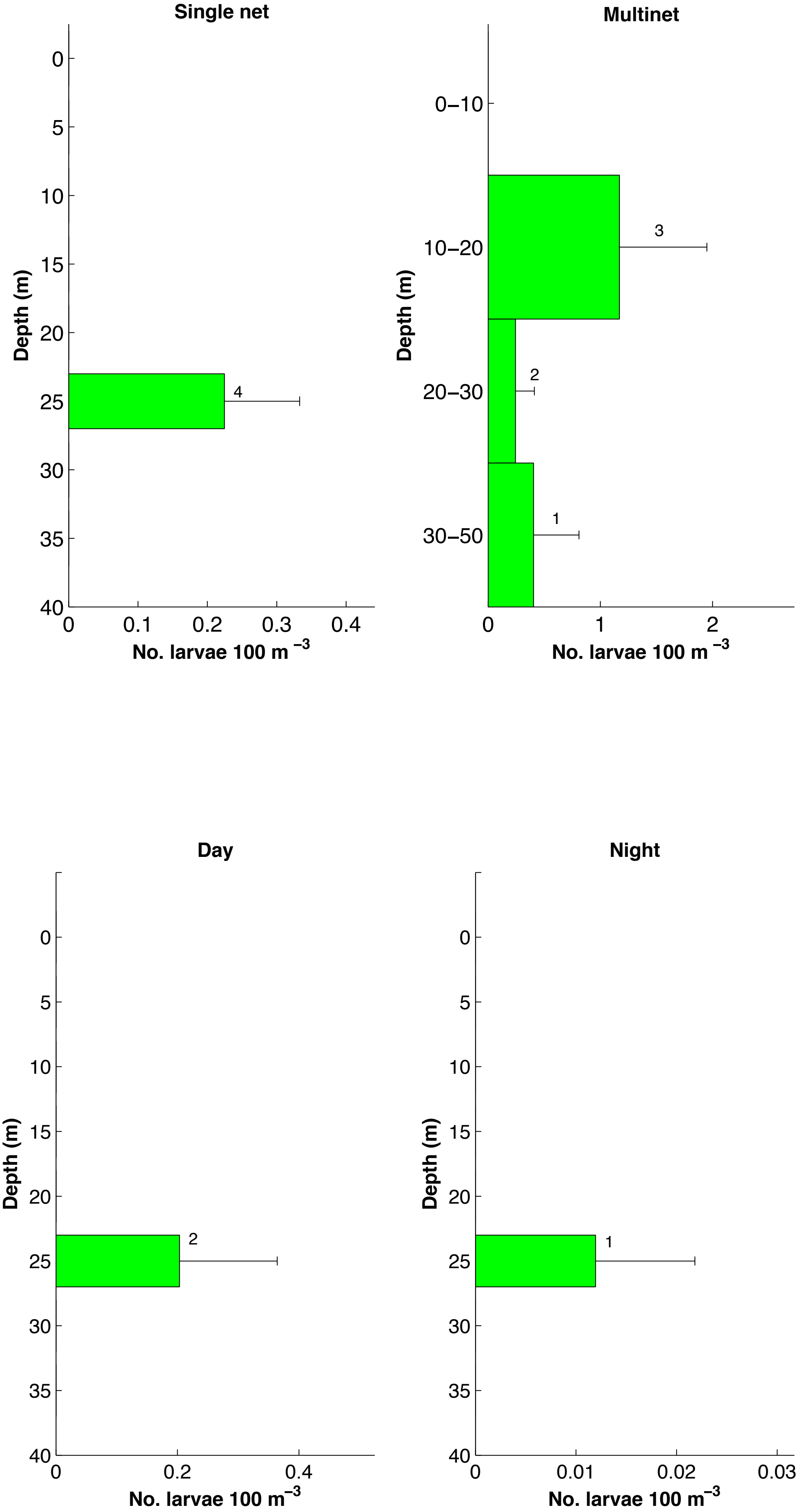


79

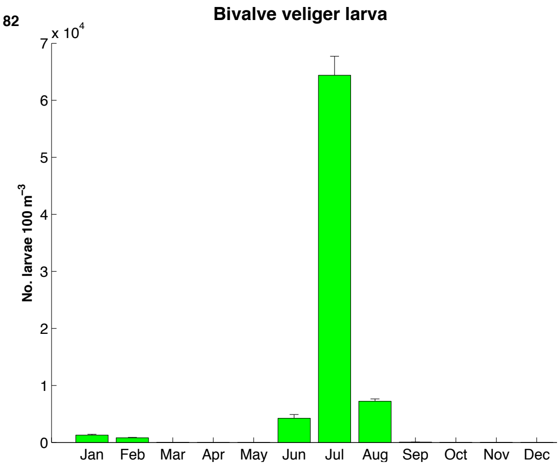
Pilumnus hurtellus (cf.) M



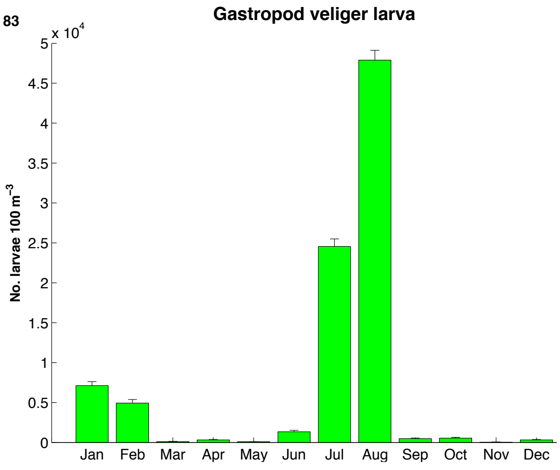
Ebalia spp. Z1–4



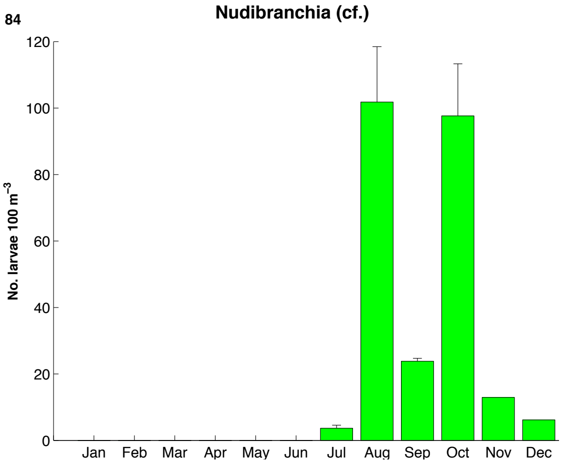
82


Bivalve veliger larva

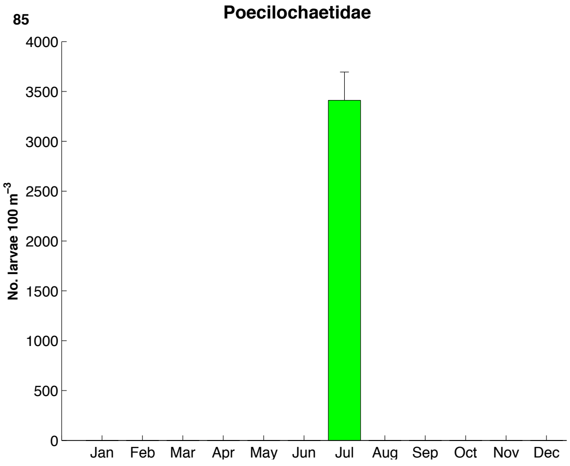
83


Gastropod veliger larva

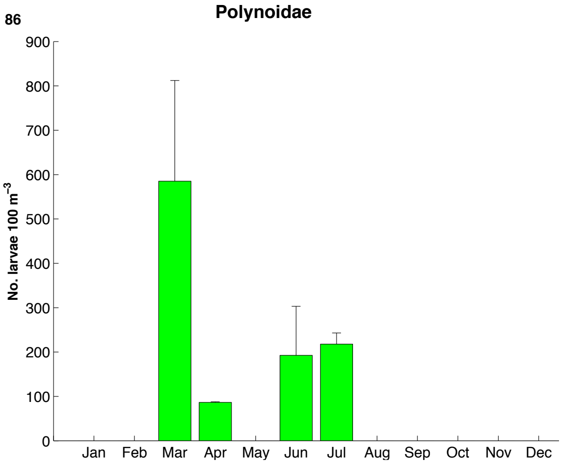
84


Nudibranchia (cf.)

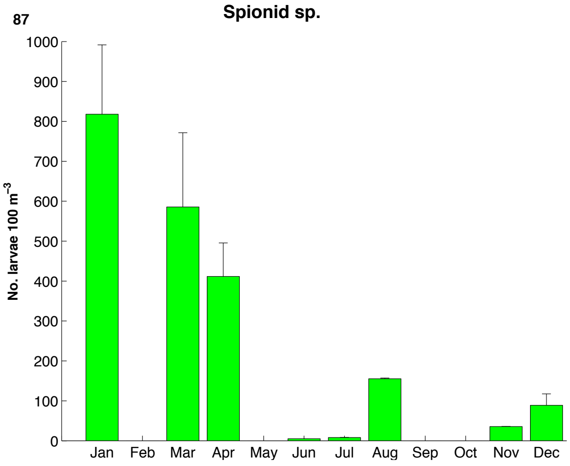
85


Poecilochaetidae

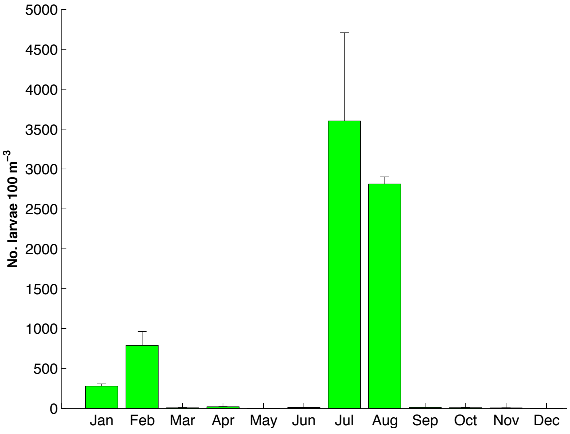
86


Polynoidae

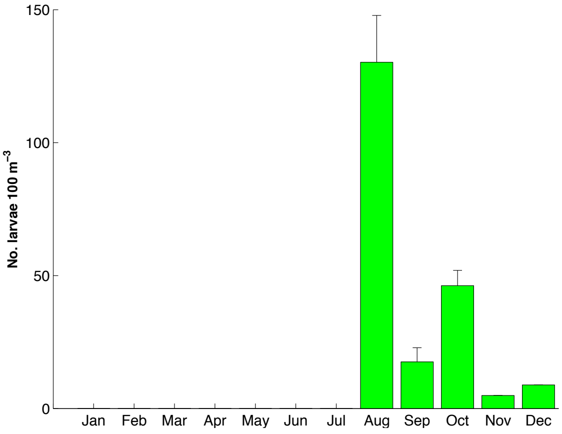
87


Spionid sp.

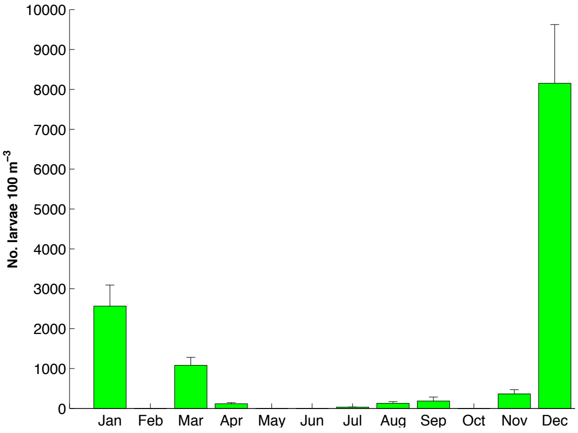
88 **Trocophore larva**



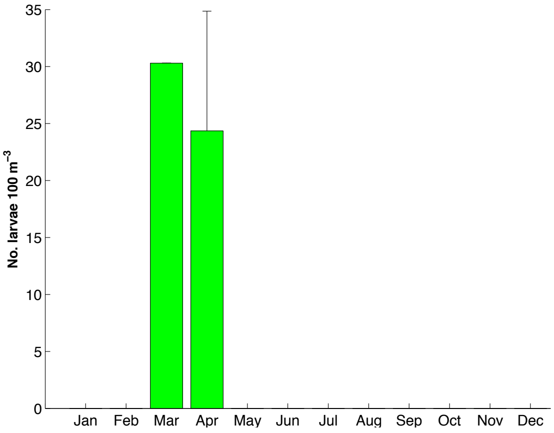
89 **Phoronid larva**



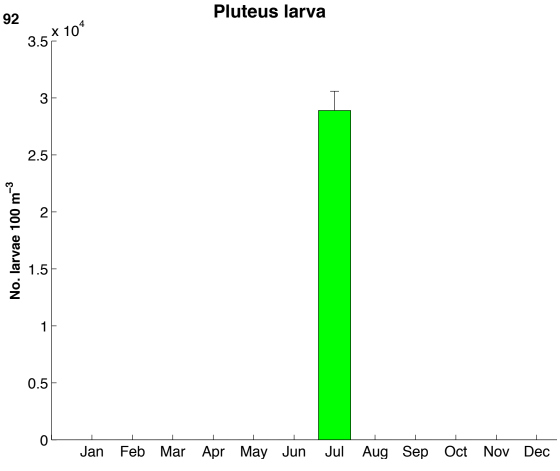
90 **Cyphonautes larva**



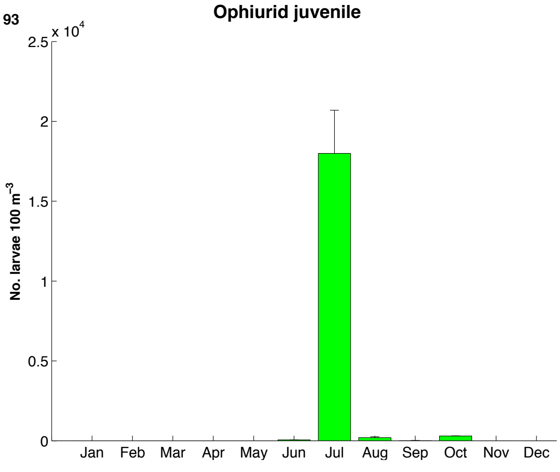
91 **Cnidaria**



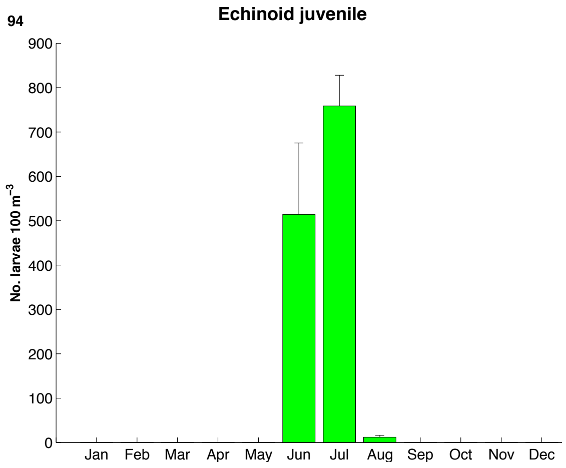
92 **Pluteus larva**



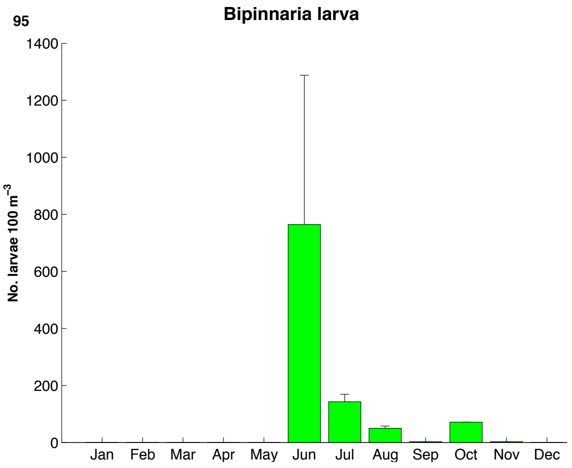
93 **Ophiurid juvenile**



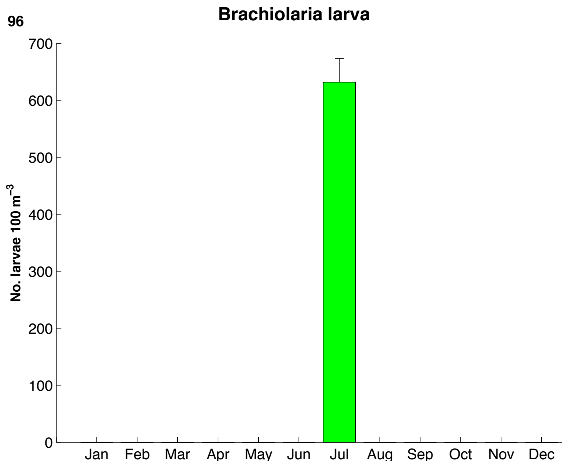
94


Echinoid juvenile

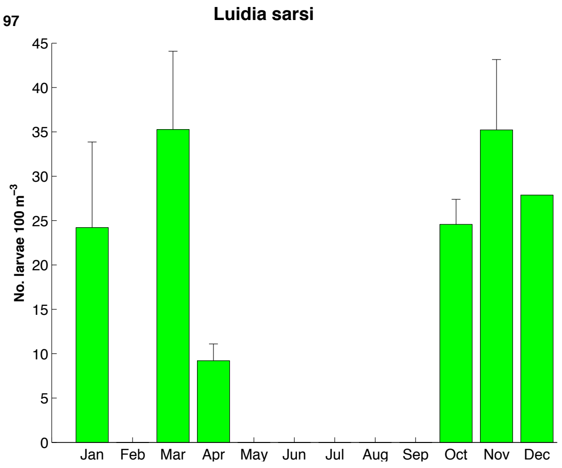
95


Bipinnaria larva

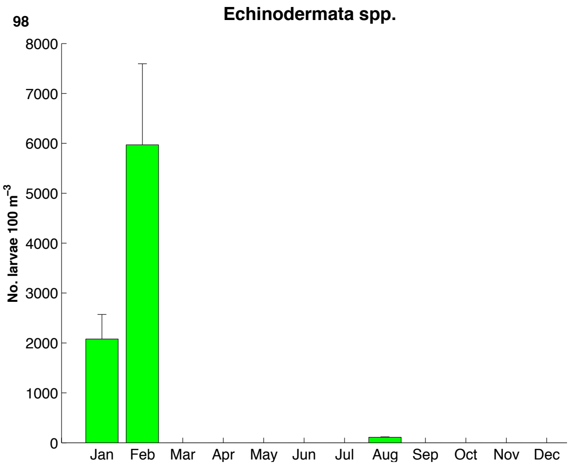
96


Brachiolaria larva

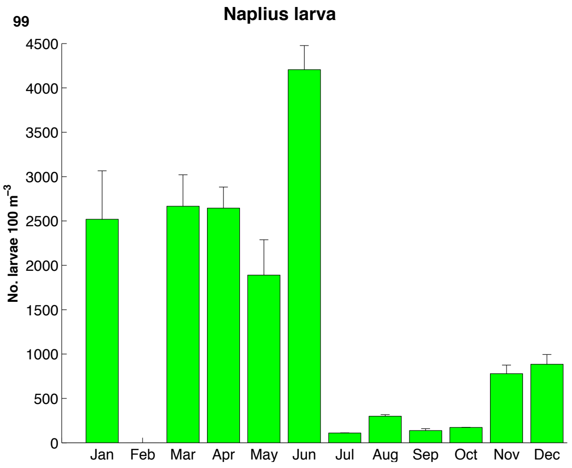
97


Luidia sarsi

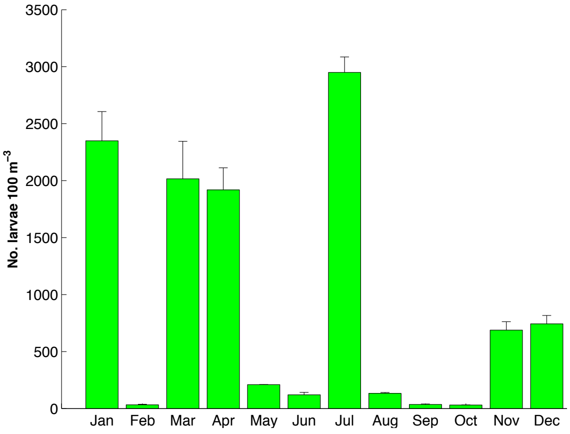
98


Echinodermata spp.

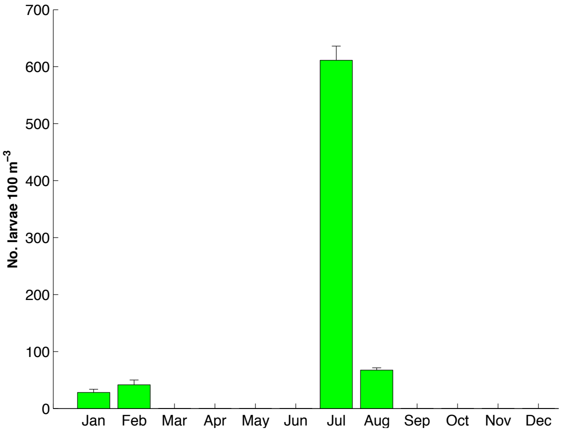
99


Naplius larva

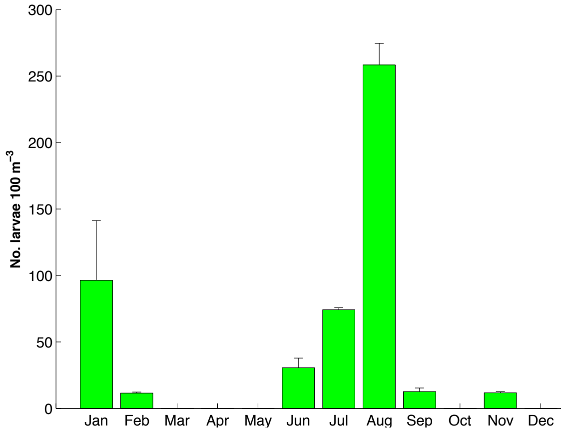
100


Cyprid larva

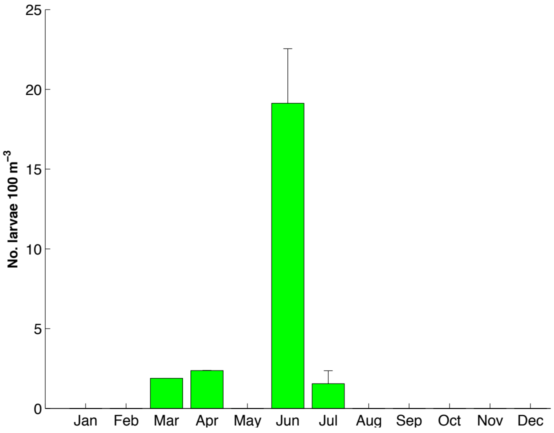
101


Palaemon sp.

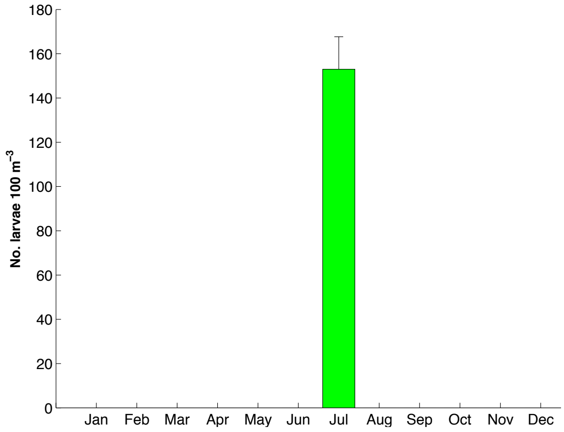
102


Crangon sp.

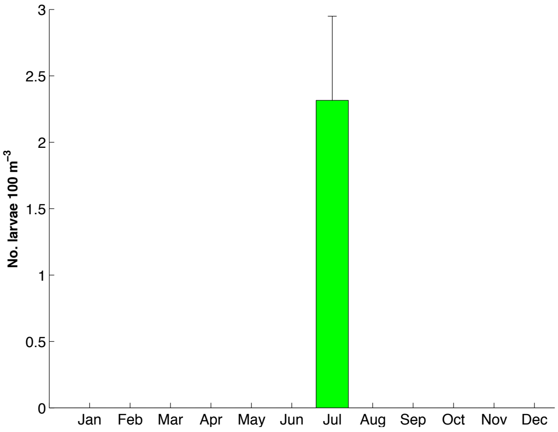
103


Philicheras bispinosus Z

104

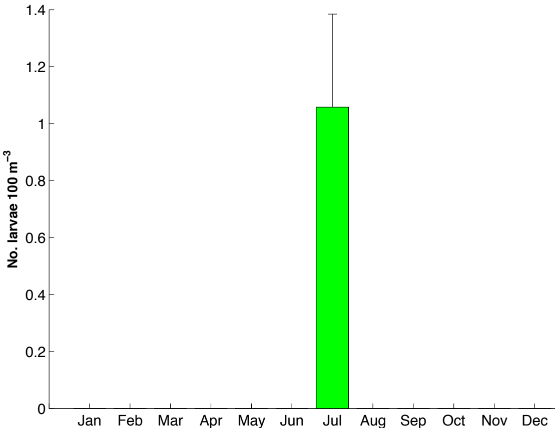

Pandalina brevirostus

105


Athanas nitescens (cf.) PL

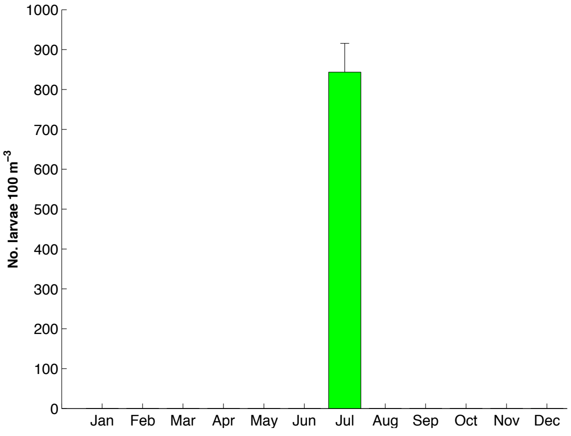
106

Alphaeid Z



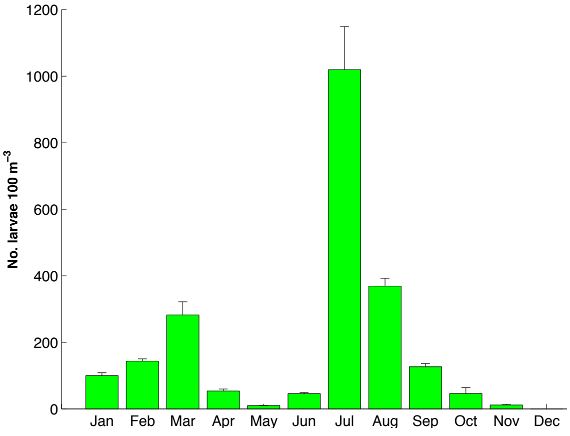
107

Hippolythid



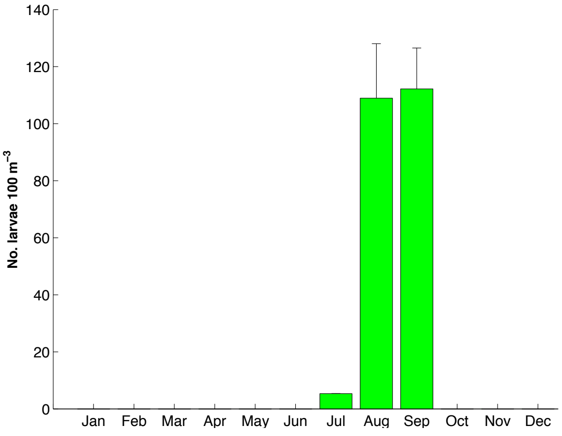
108

Caridea spp.



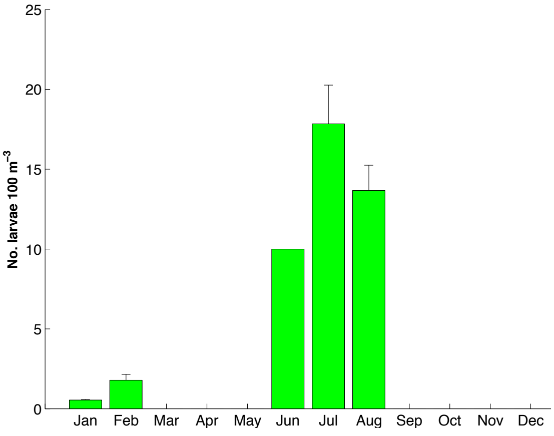
109

Callianassa sp.



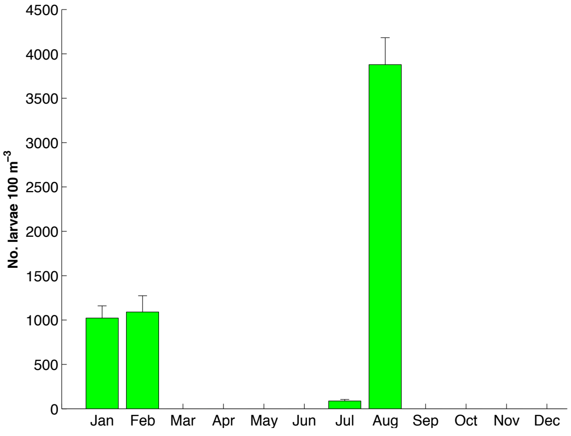
110

Upogebia sp.



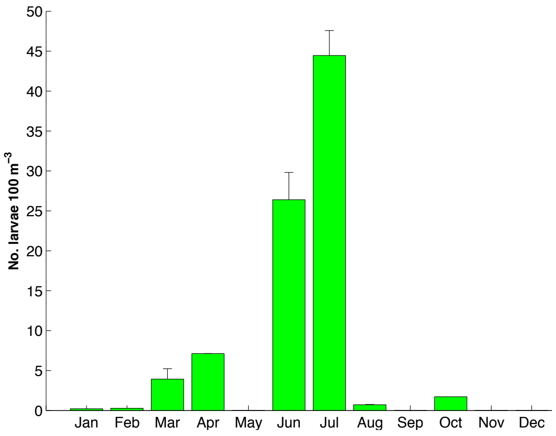
111

Calocaris sp.



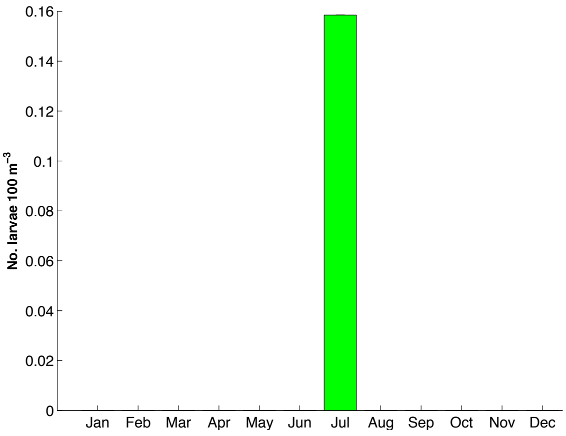
112

Nephrops norvegicus



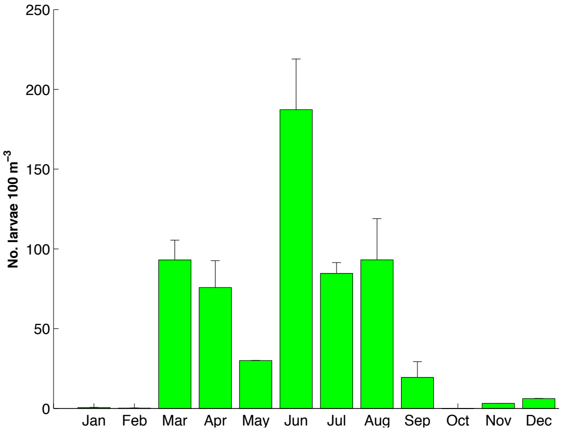
113

Homarus gammarus



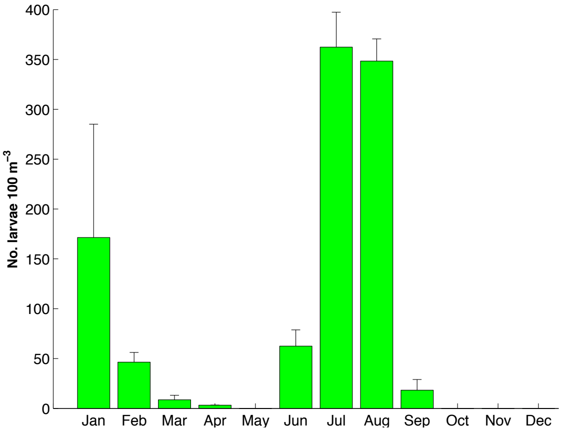
114

Pagurid



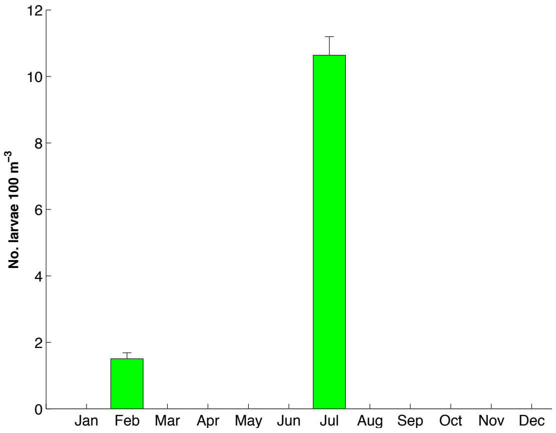
115

Galathea sp.



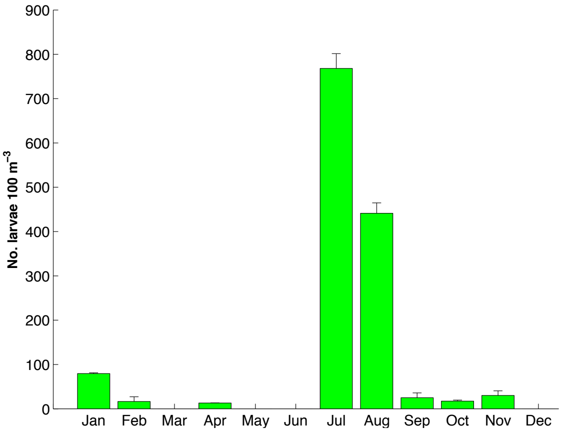
116

Munidopsis sp.

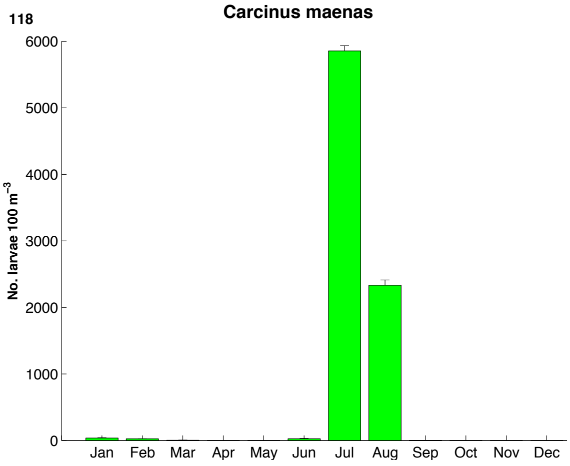


117

Pisidia longicornis (cf.)

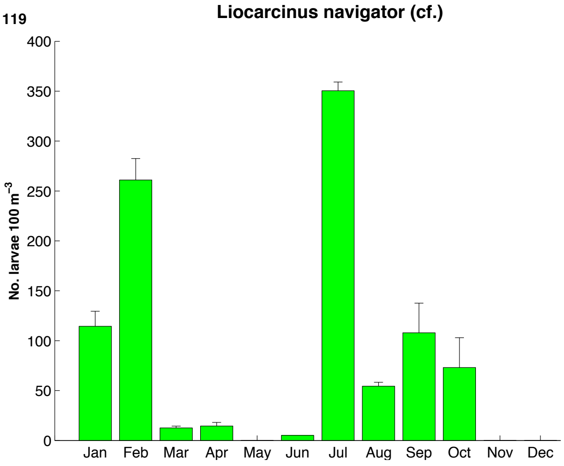


118



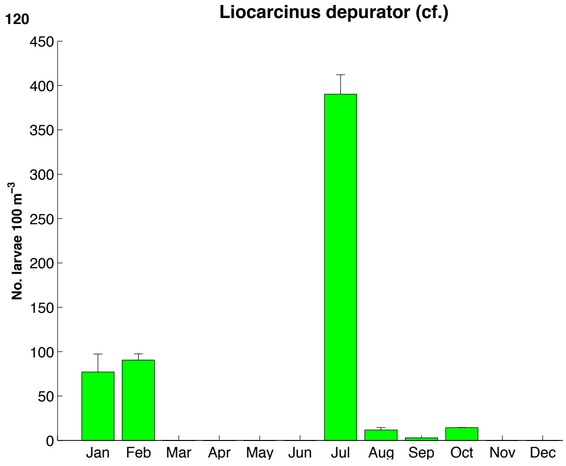
Carcinus maenas

119



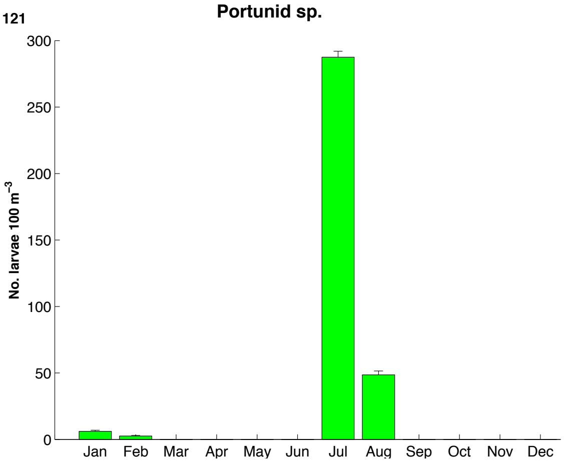
Liocarcinus navigator (cf.)

120



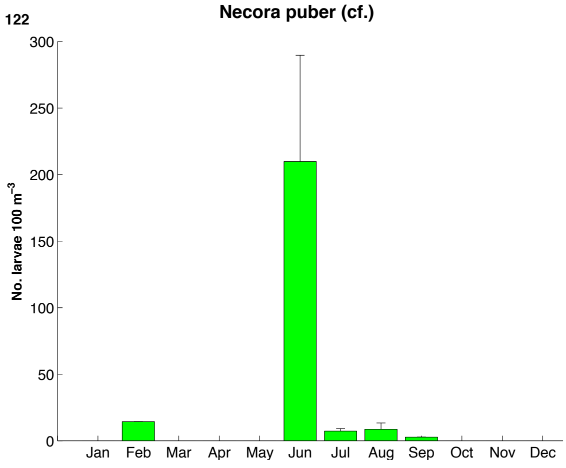
Liocarcinus depurator (cf.)

121



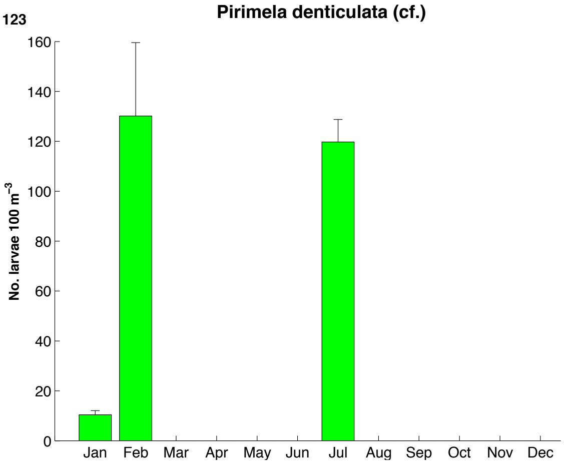
Portunid sp.

122



Necora puber (cf.)

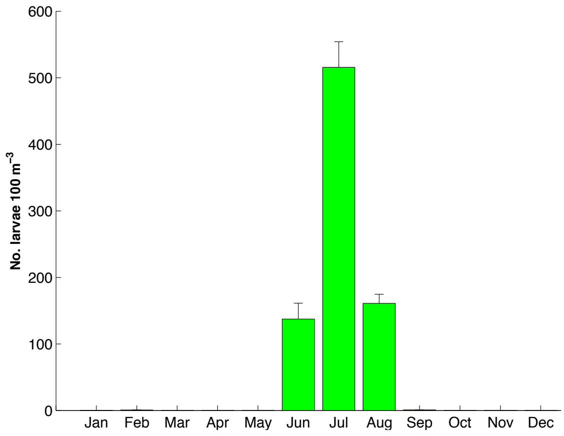
123



Pirimela denticulata (cf.)

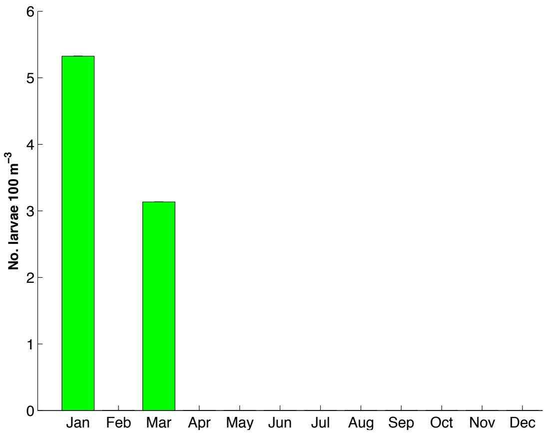
124

Cancer pagurus



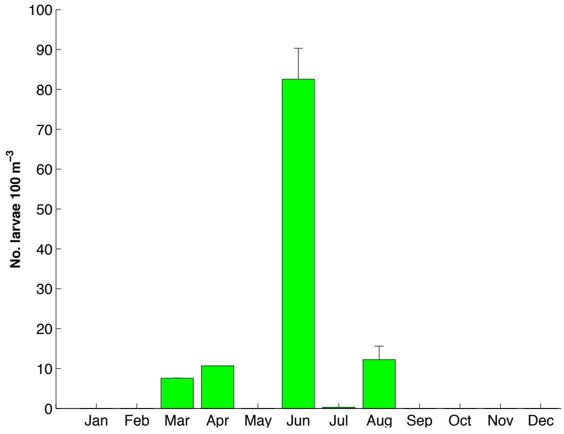
125

Thia scutella (cf.)



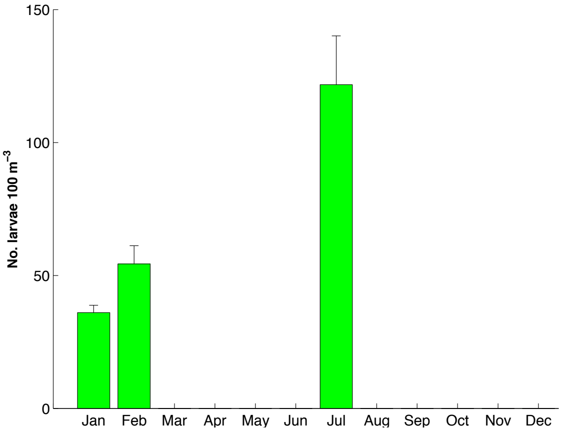
126

Corystes cassivelaunus



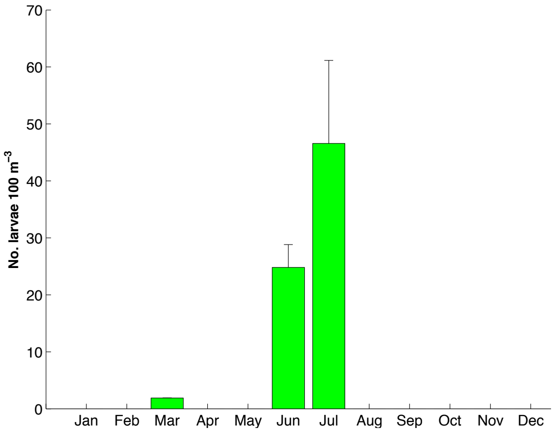
127

Atelecyclus rotundatus



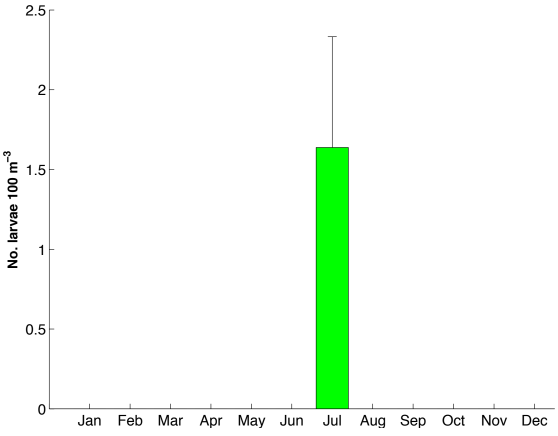
128

Hyas spp.

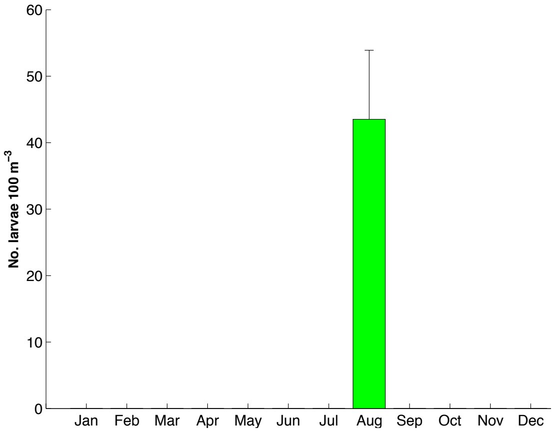


129

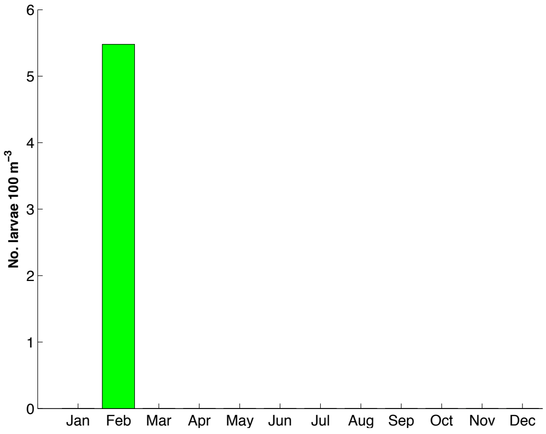
Macropodia rostrata



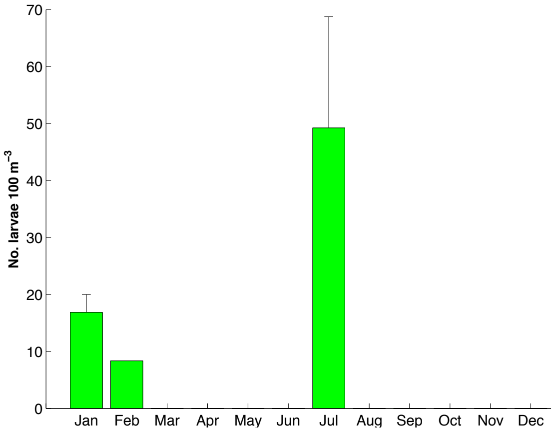
130 **Euronyme spp. (cf.)**



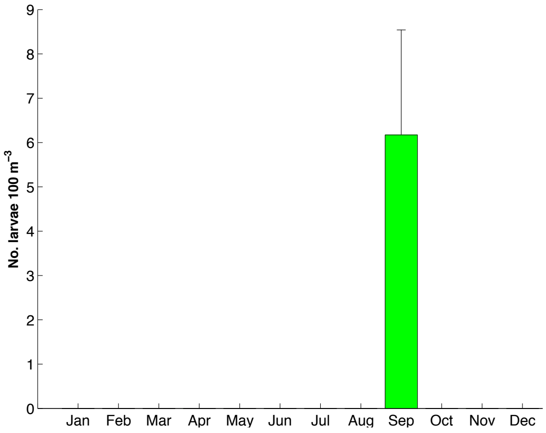
131 **Pinnotheres pisum (cf.)**



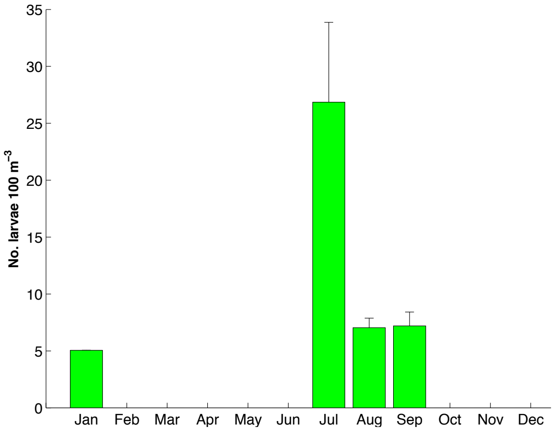
132 **Geryon trispinosus (cf.)**



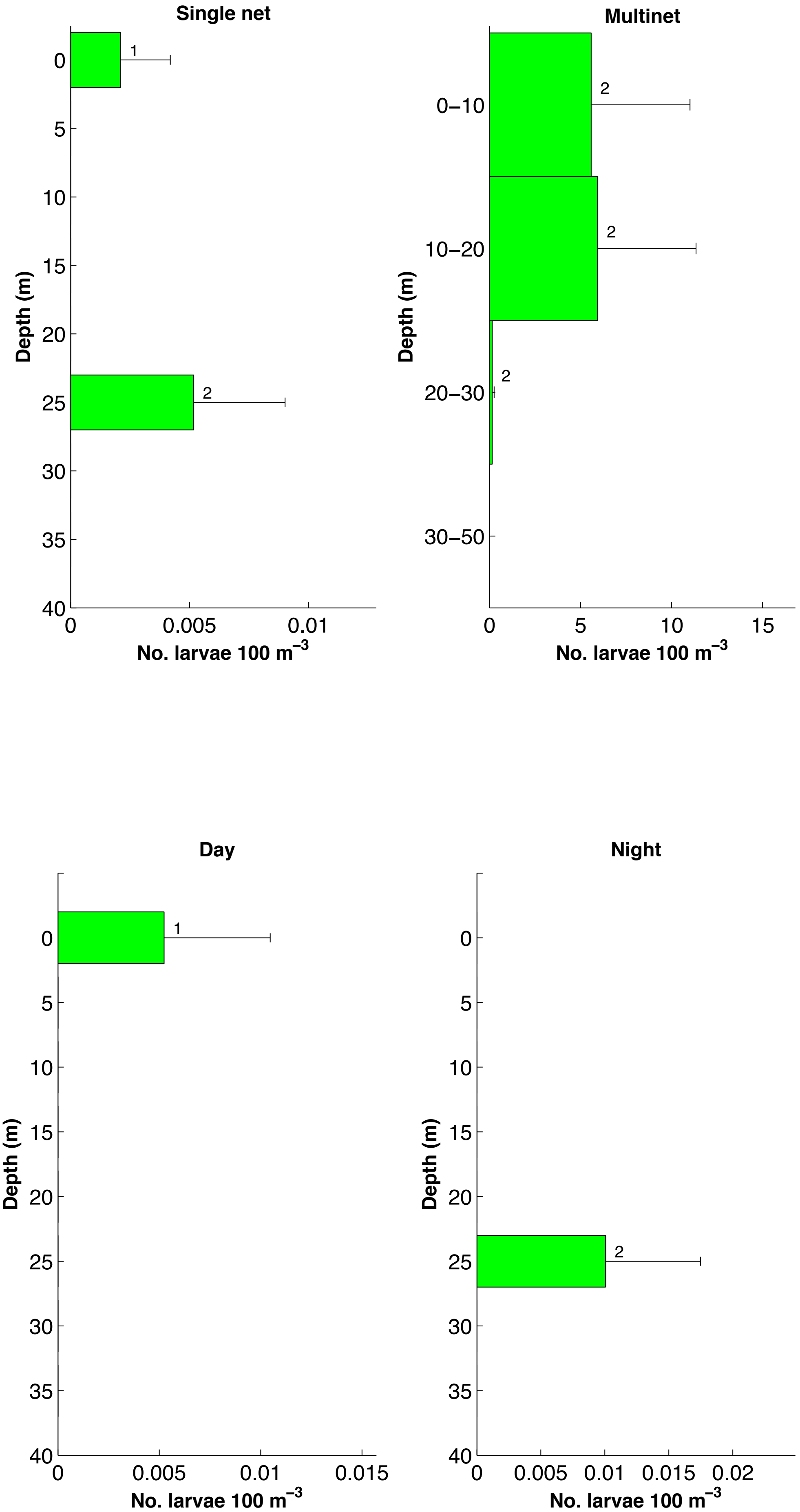
133 **Pilumnus hurtellus (cf.)**



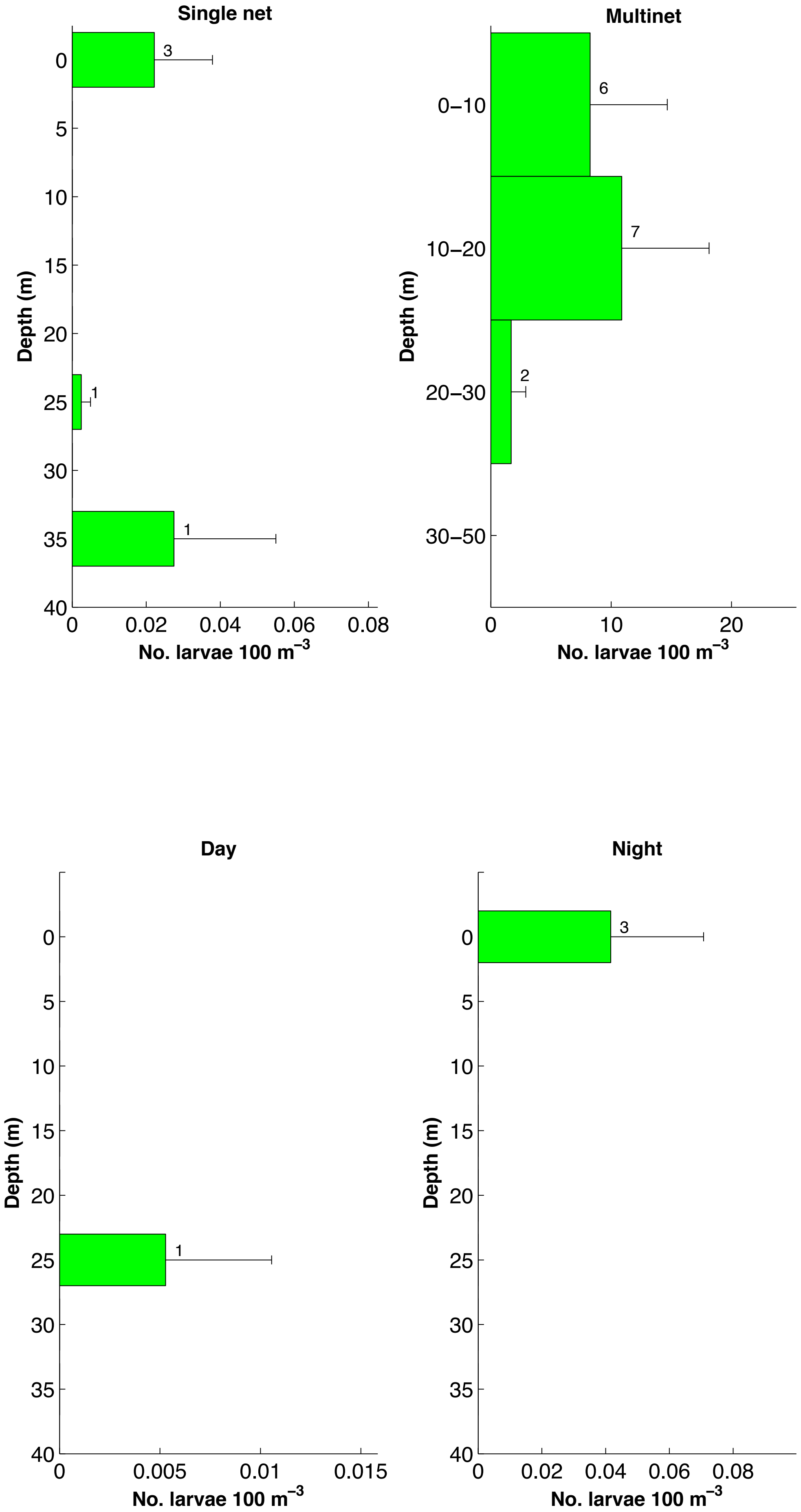
134 **Ebalia spp.**



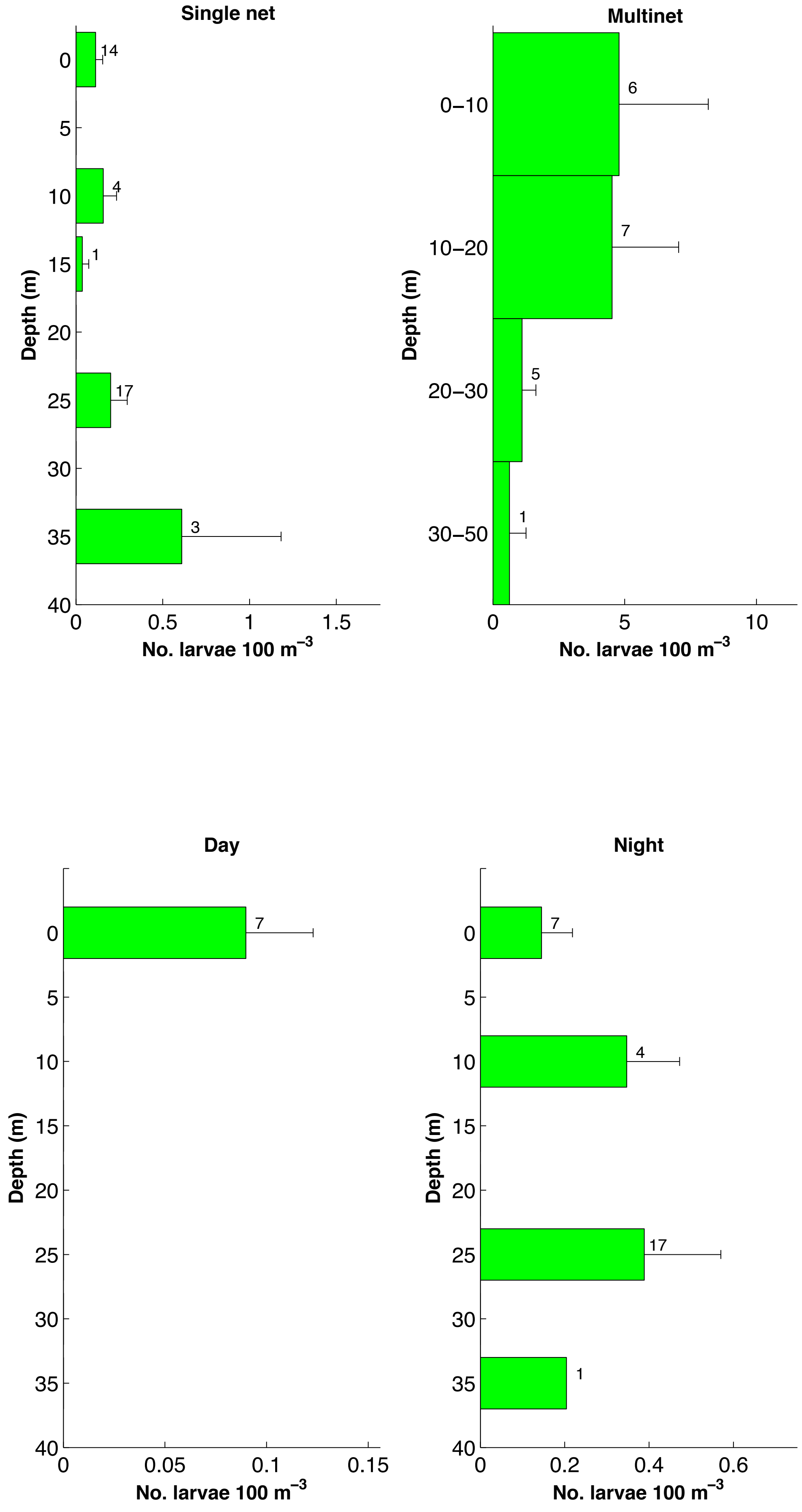
Sprattus sprattus



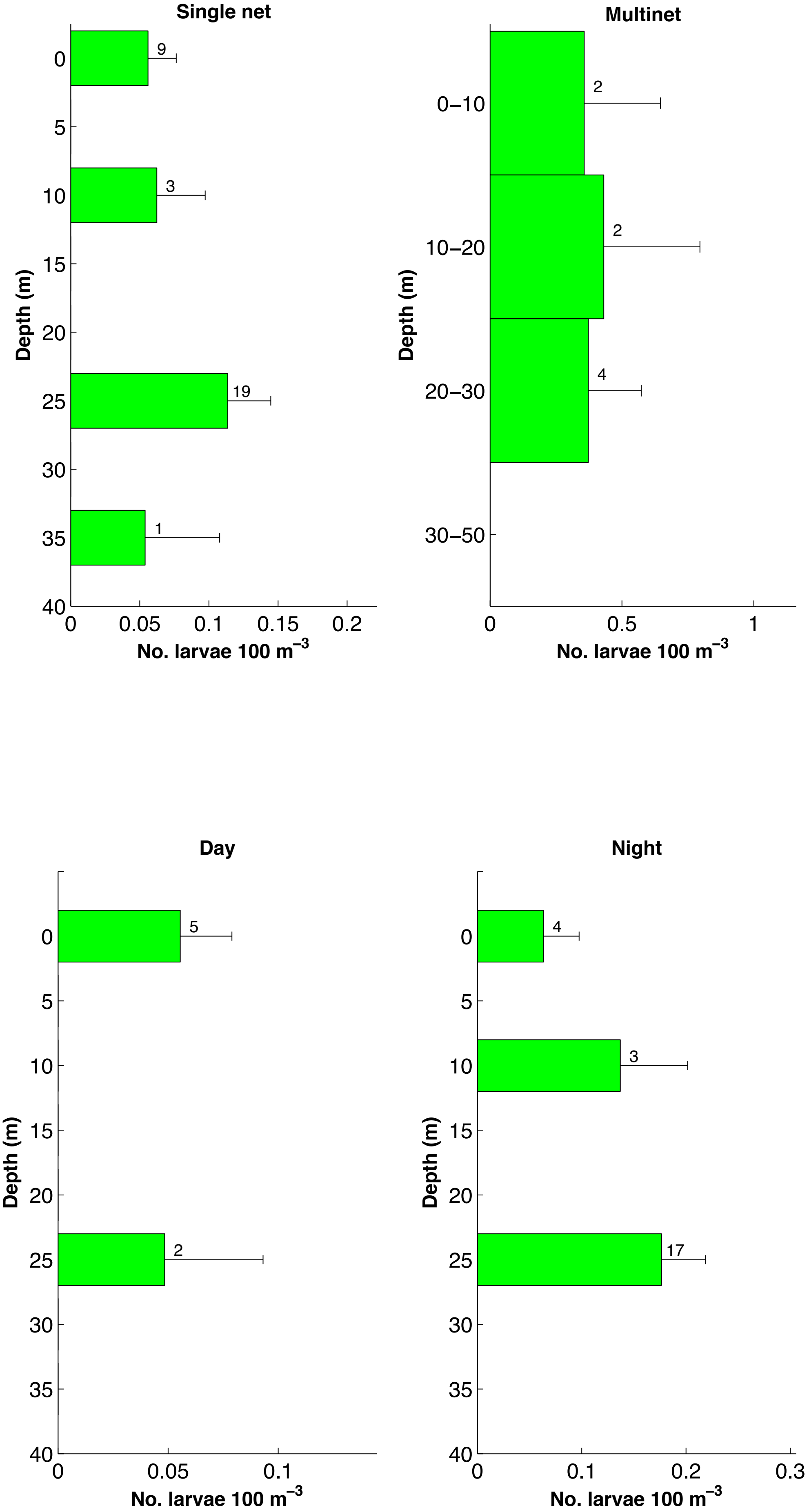
Clupeidae < 5


Single net
Depth (m)
0
5
10
15
20
25
30
35
40
3
1
1
0
0.02
0.04
0.06
0.08
No. larvae 100 m^{-3}
Multinet
Depth (m)
0–10
10–20
20–30
30–50
6
7
2
0
10
20
No. larvae 100 m^{-3}
Day
Depth (m)
0
5
10
15
20
25
30
35
40
1
0
0.005
0.01
0.015
No. larvae 100 m^{-3}
Night
Depth (m)
0
5
10
15
20
25
30
35
40
3
0
0.02
0.04
0.06
0.08
No. larvae 100 m^{-3}

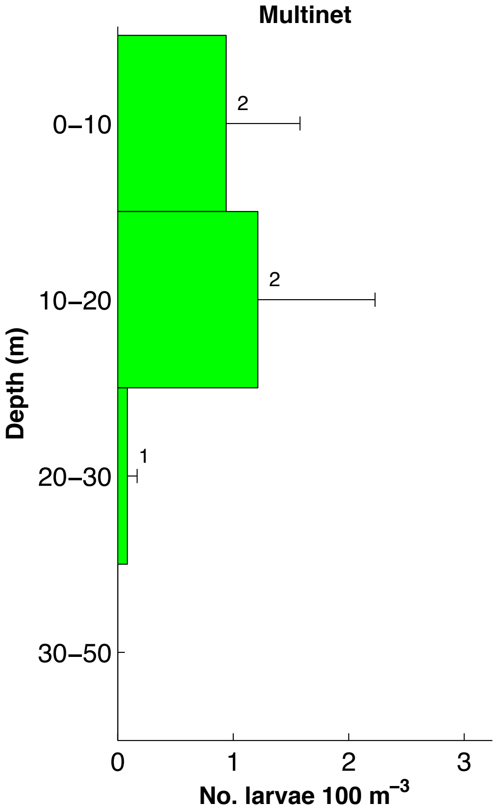
Clupeidae (6–10)



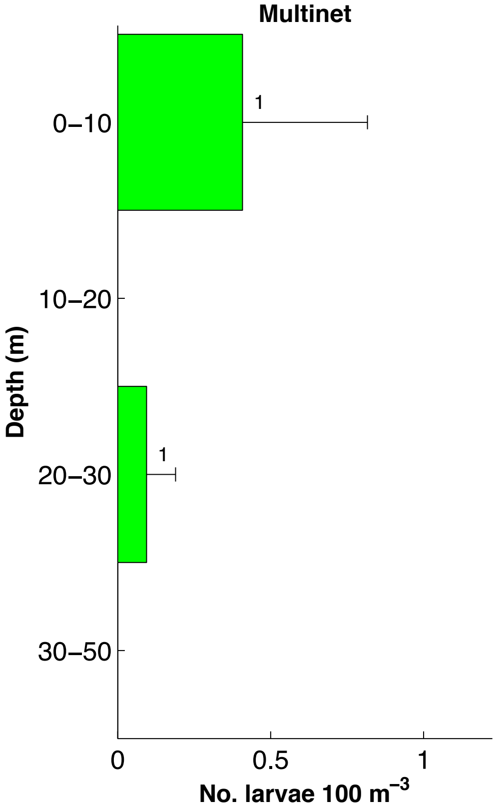
Clupeidae > 10



Gadus morhua

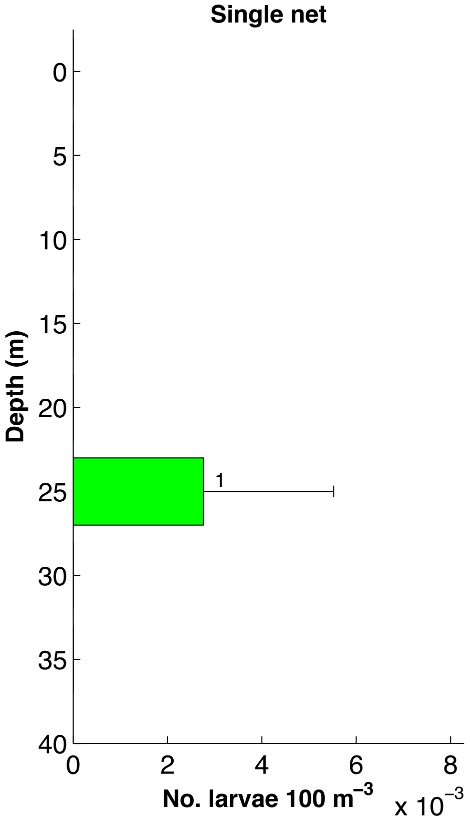


Merlangius merlangus



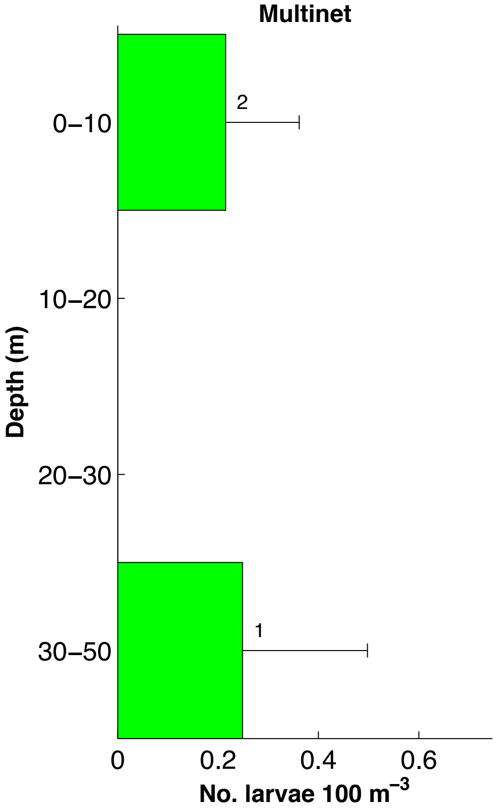
140

Raniceps raninus

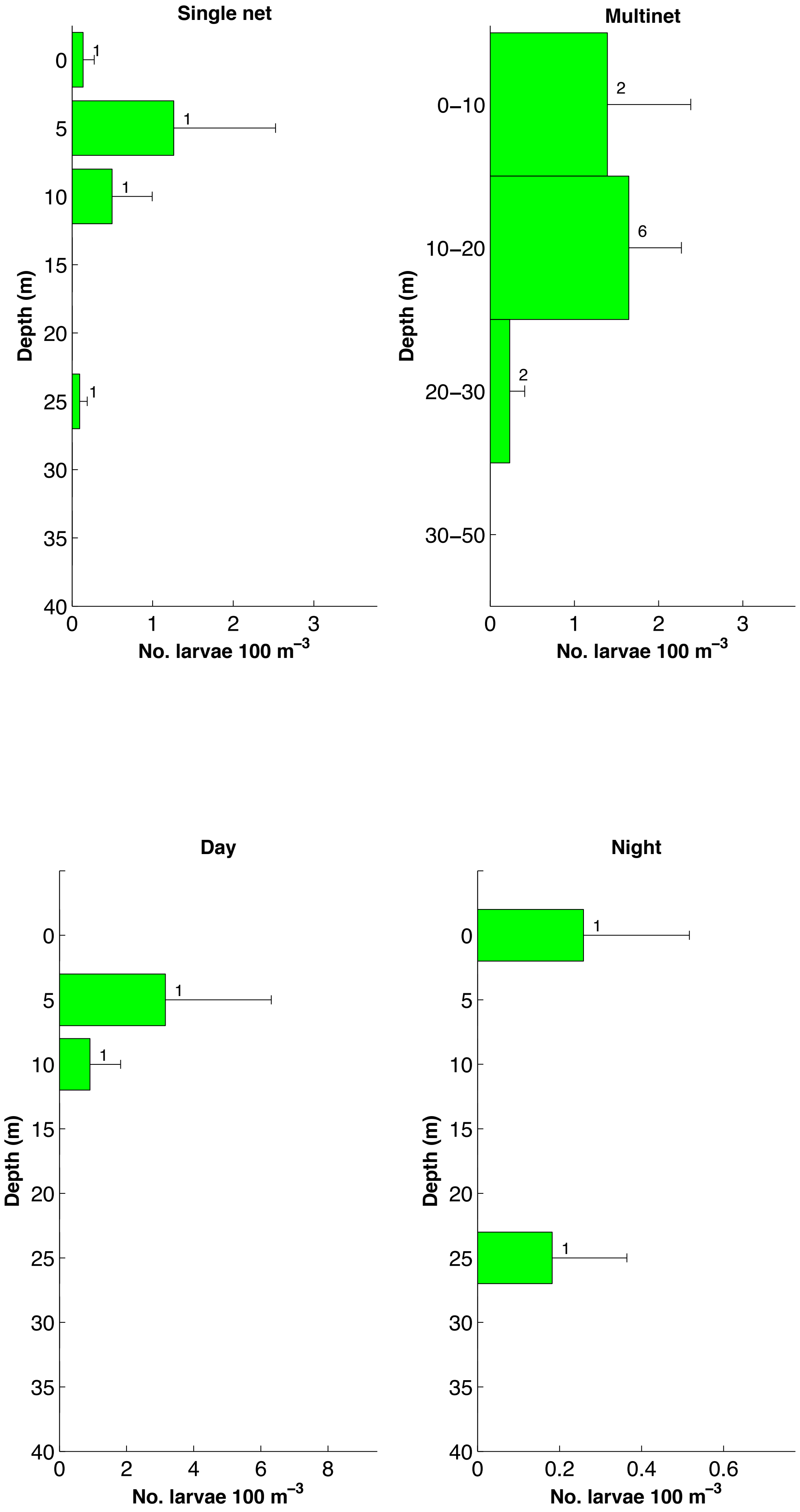


141

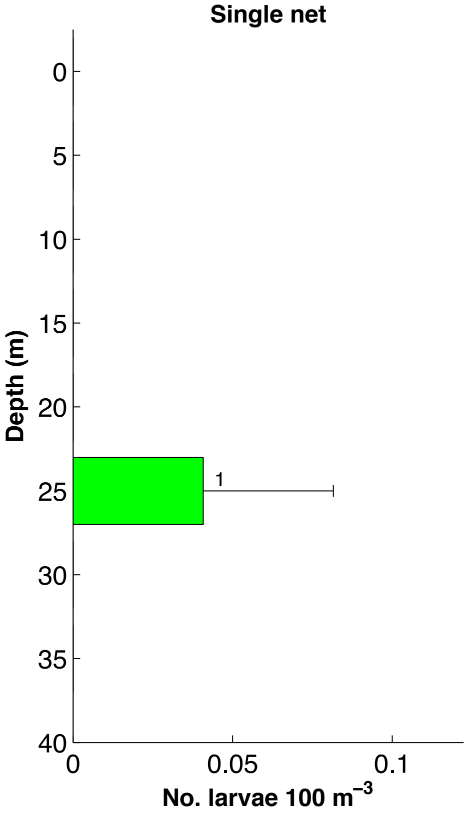
Phycidae

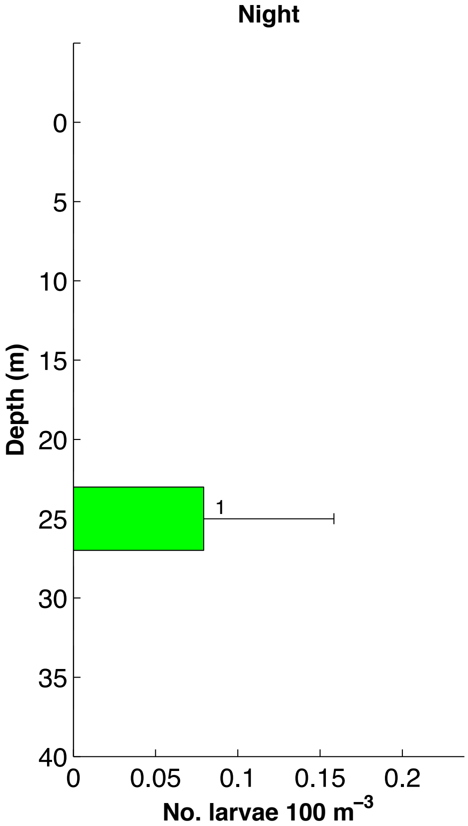


Enchelyopus cimbrius

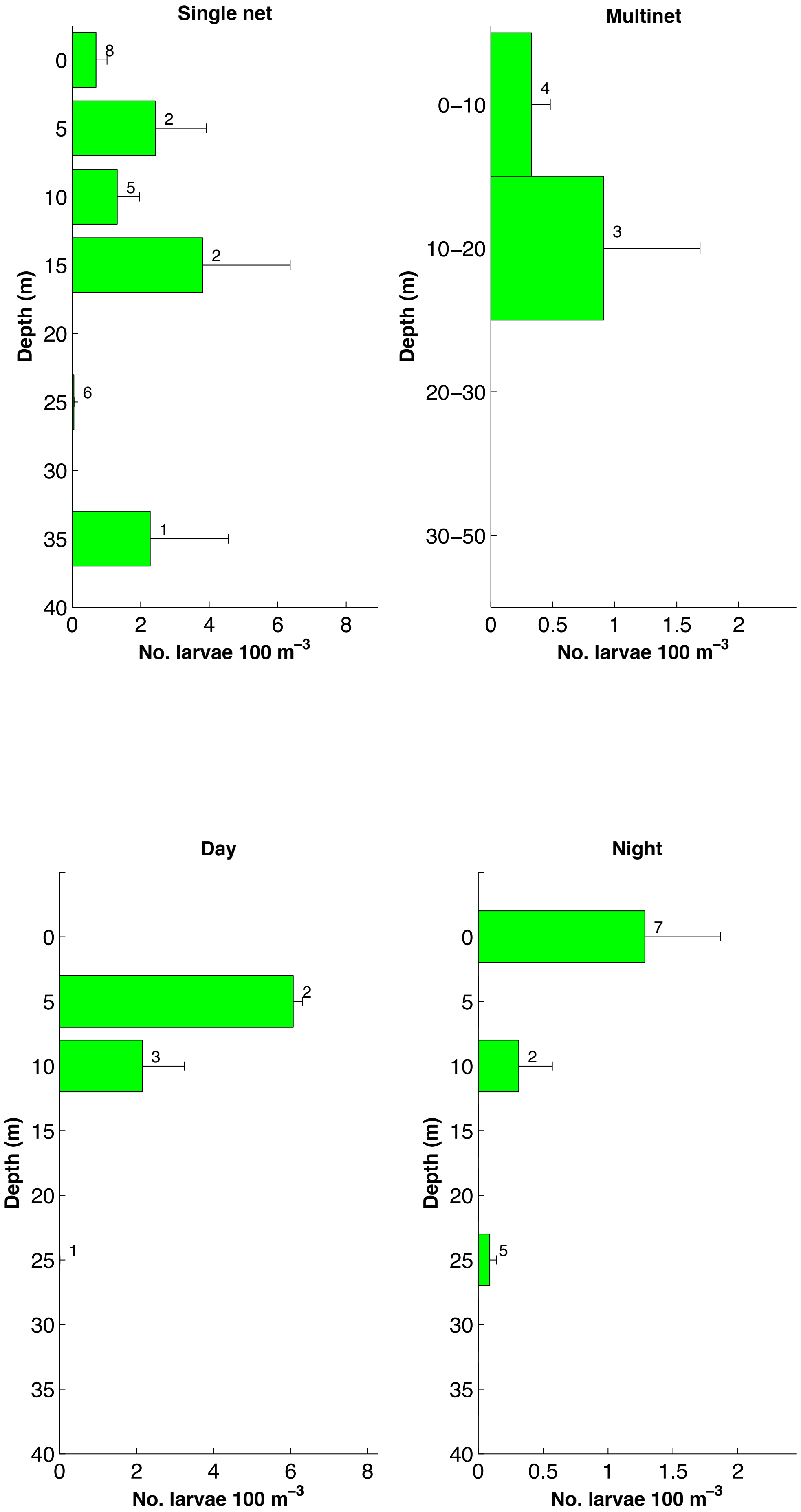


Merluccius merluccius





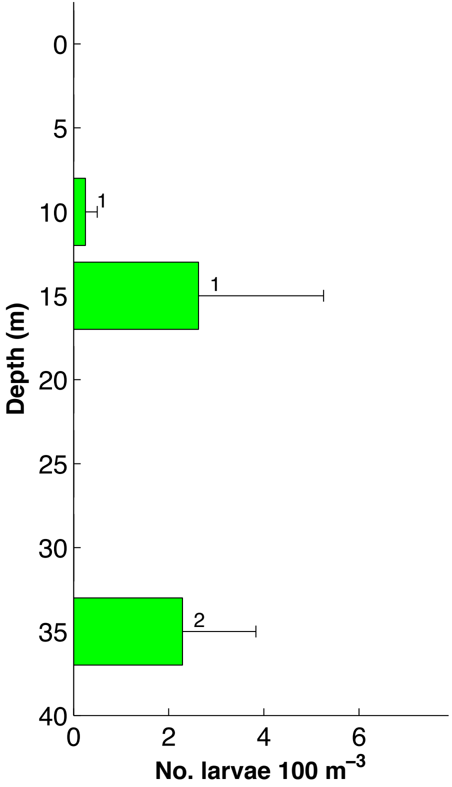
Ctenolabrus rupestris



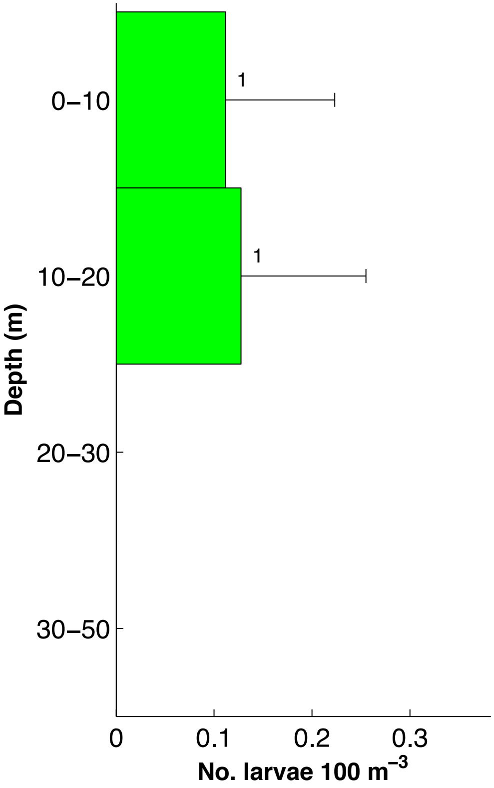
145

Labrus sp.

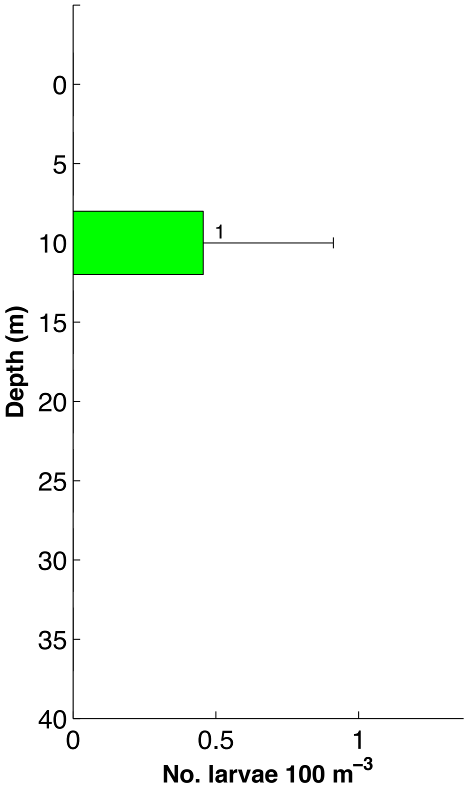
Single net



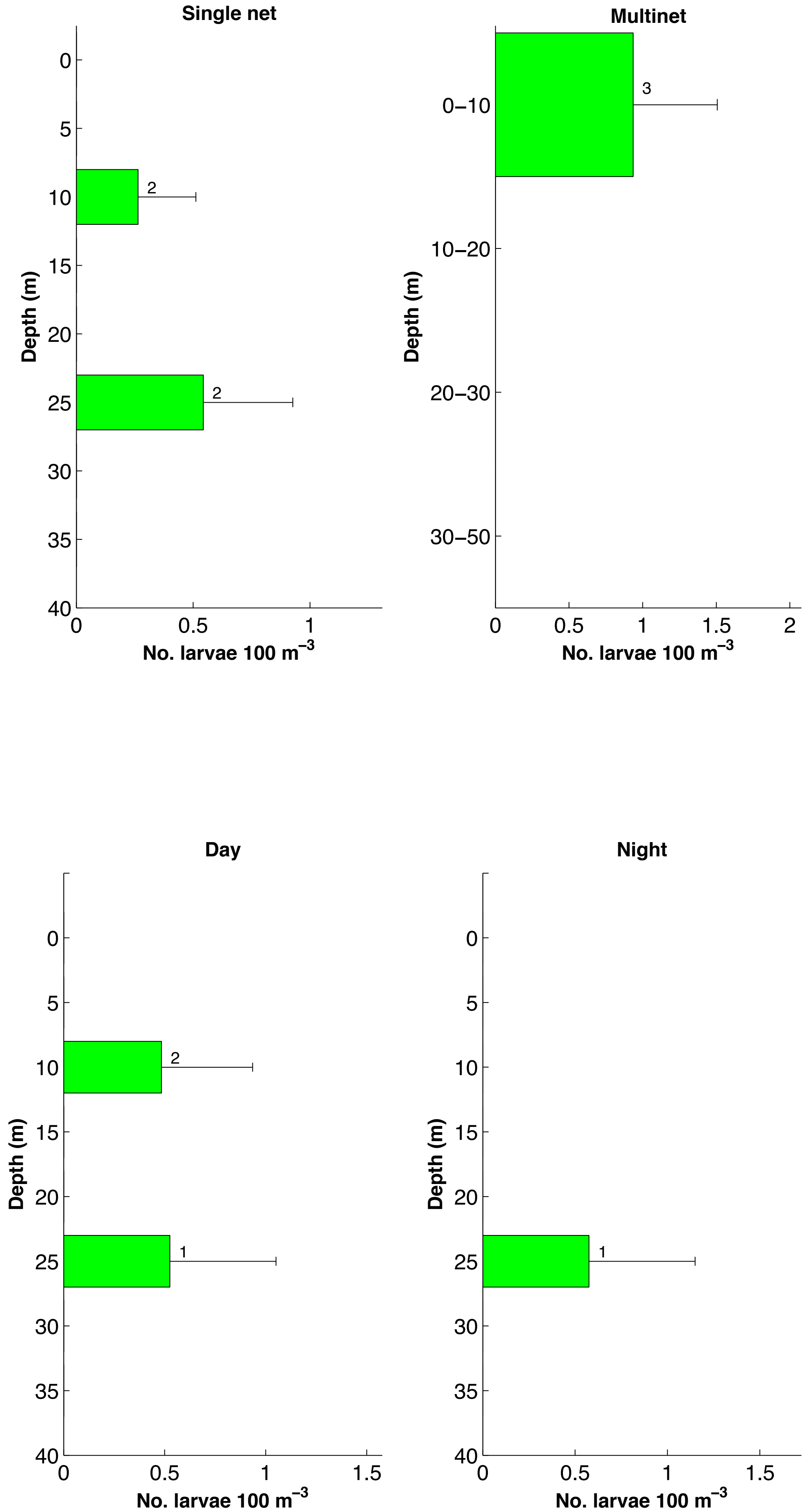
Multinet



Day

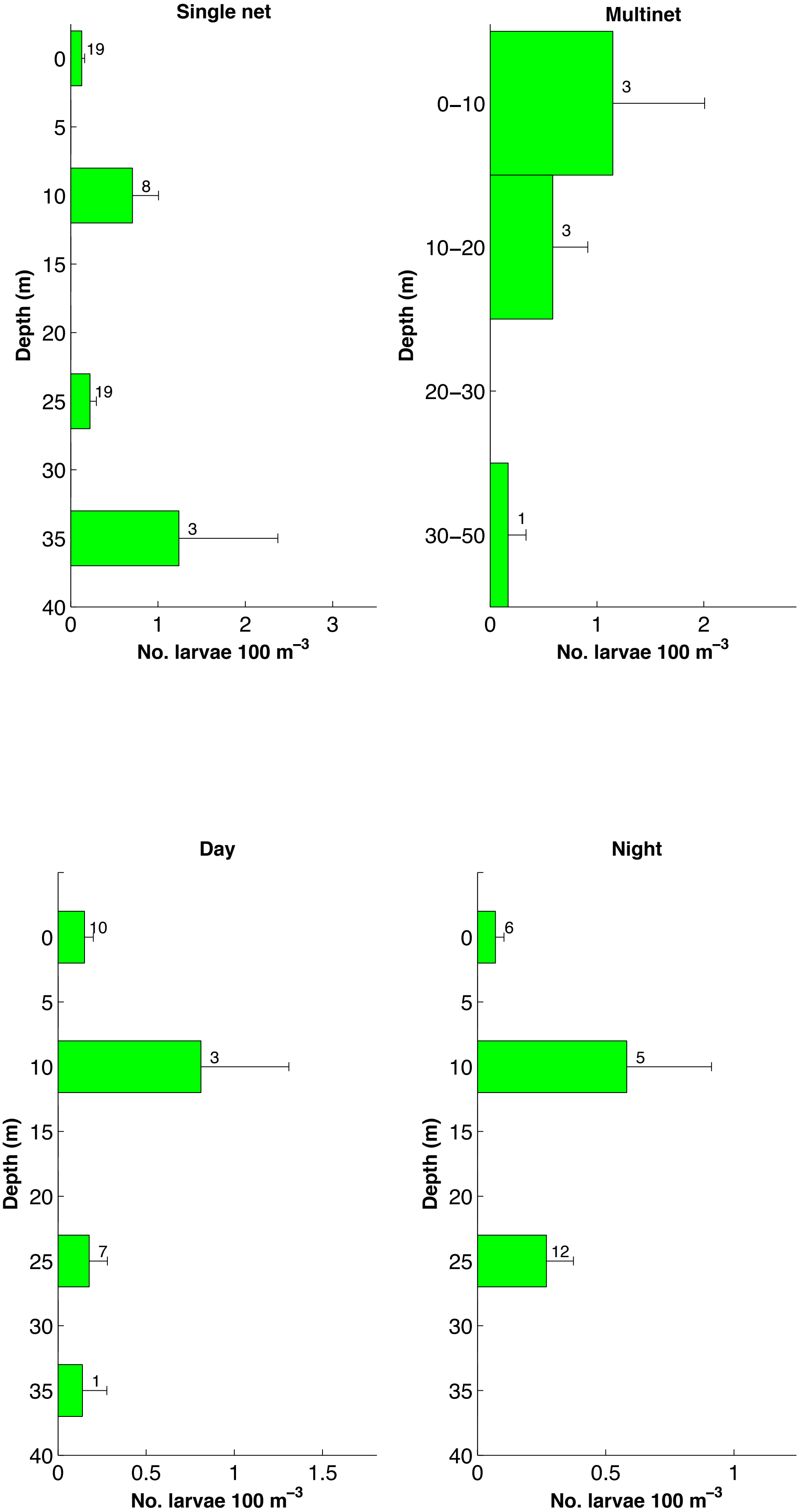


Symphodus sp.

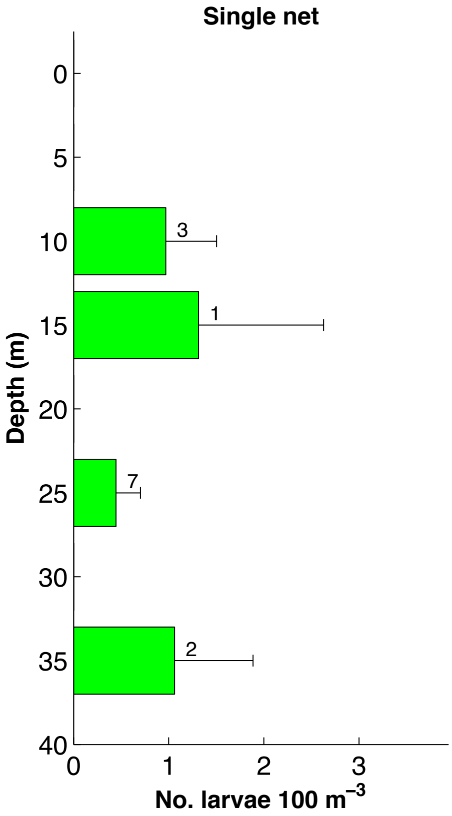


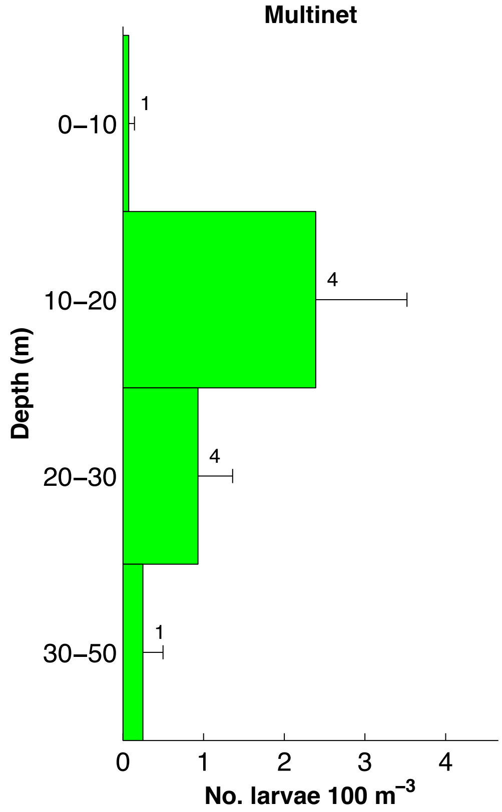
147

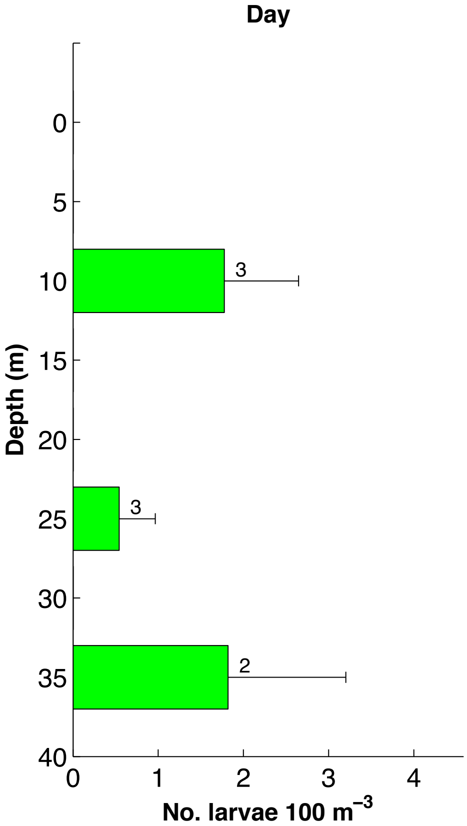
Ammodytes lancea

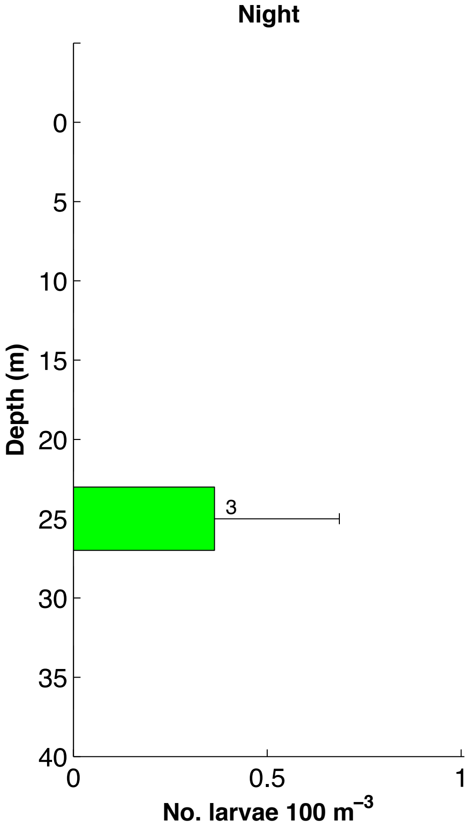


Callionymus sp.


Single net

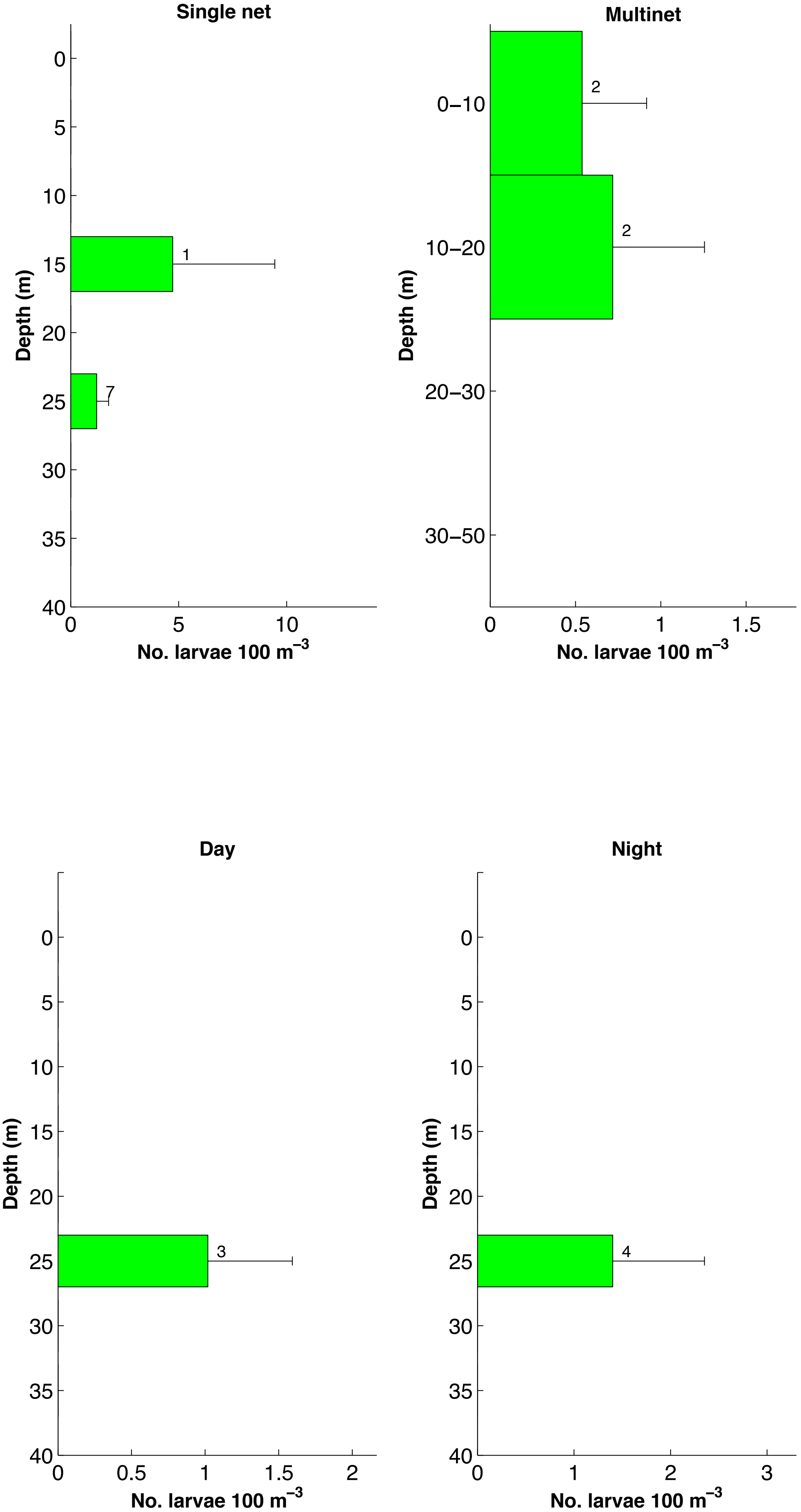

Multinet


Day

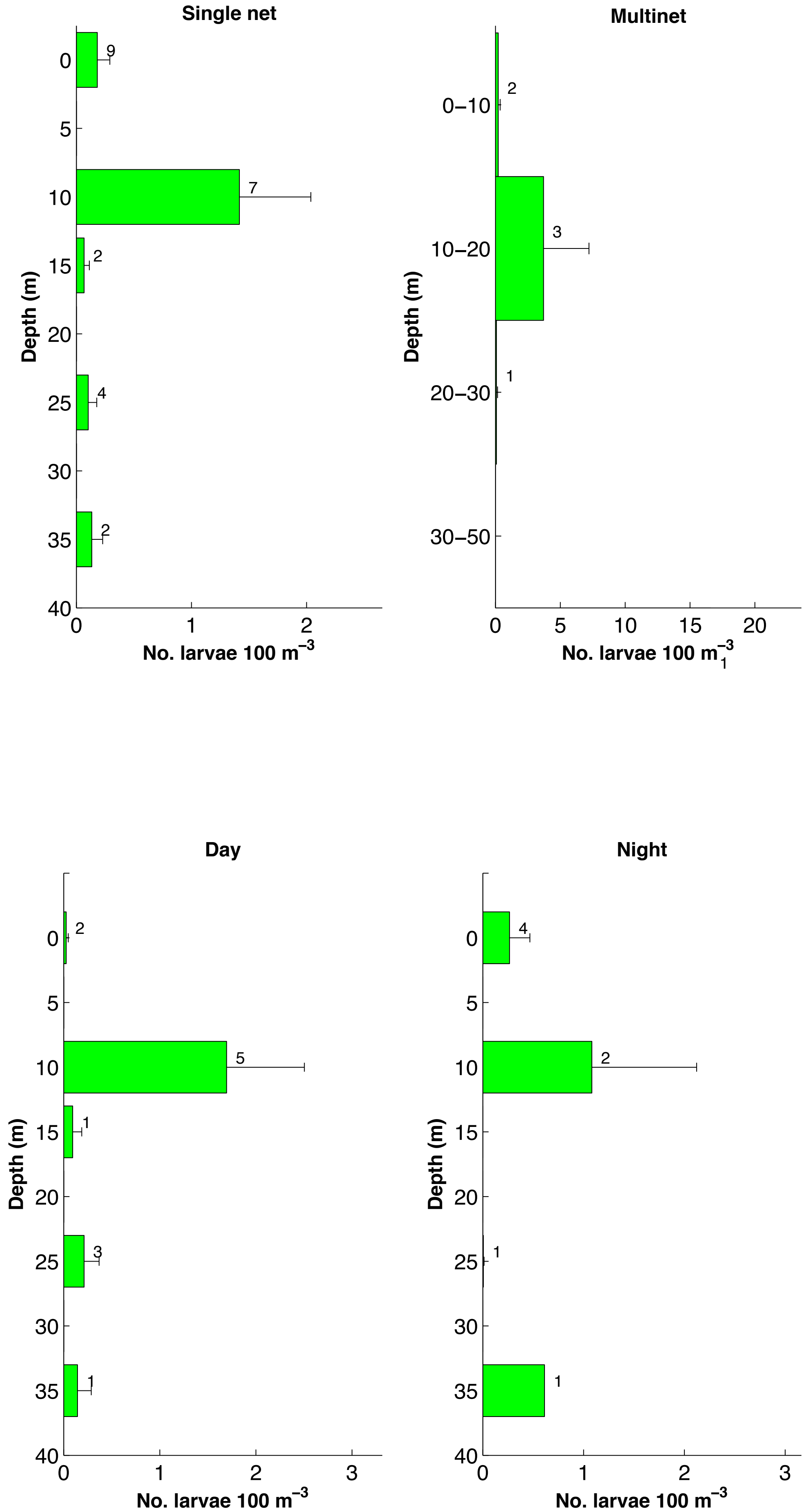

Night

149

Callionymus/Carangidae

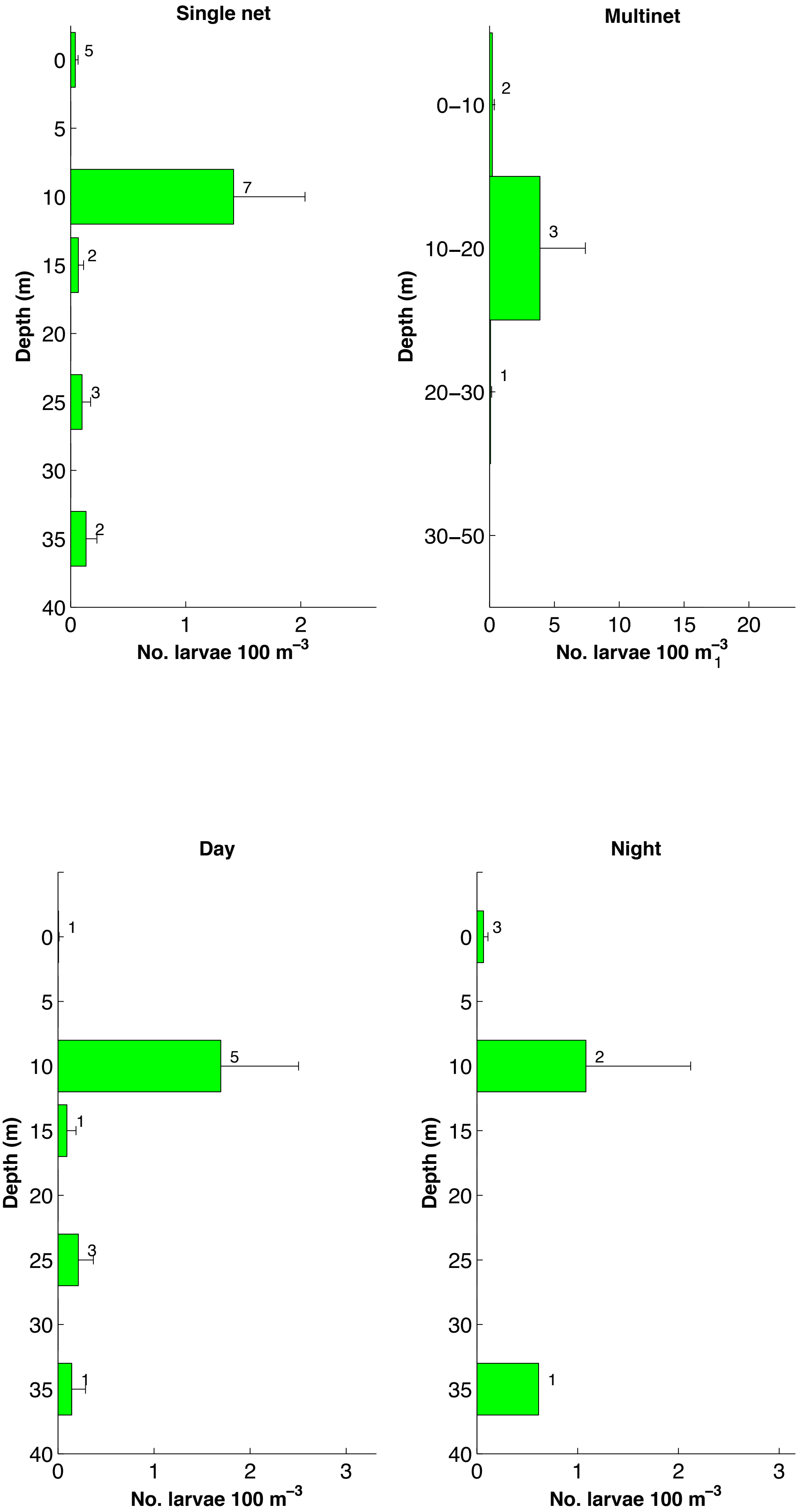


Trachurus trachurus

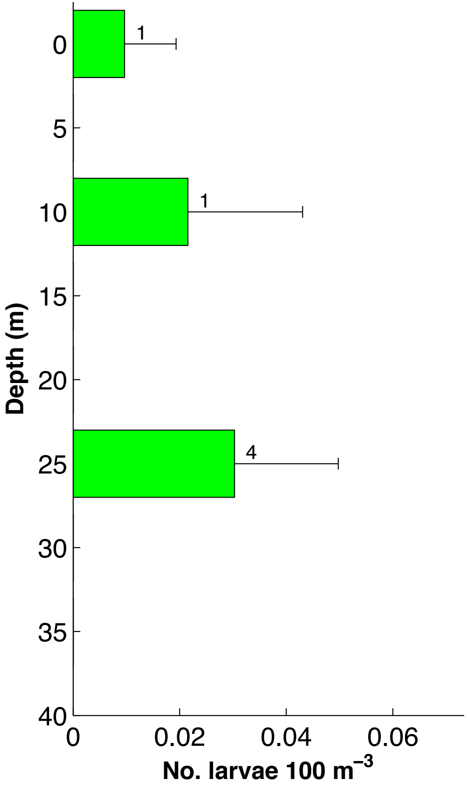


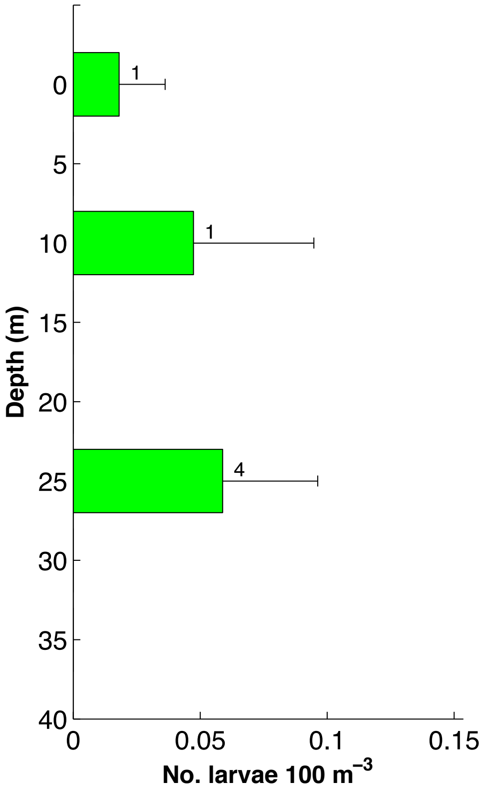
151

Carangidae



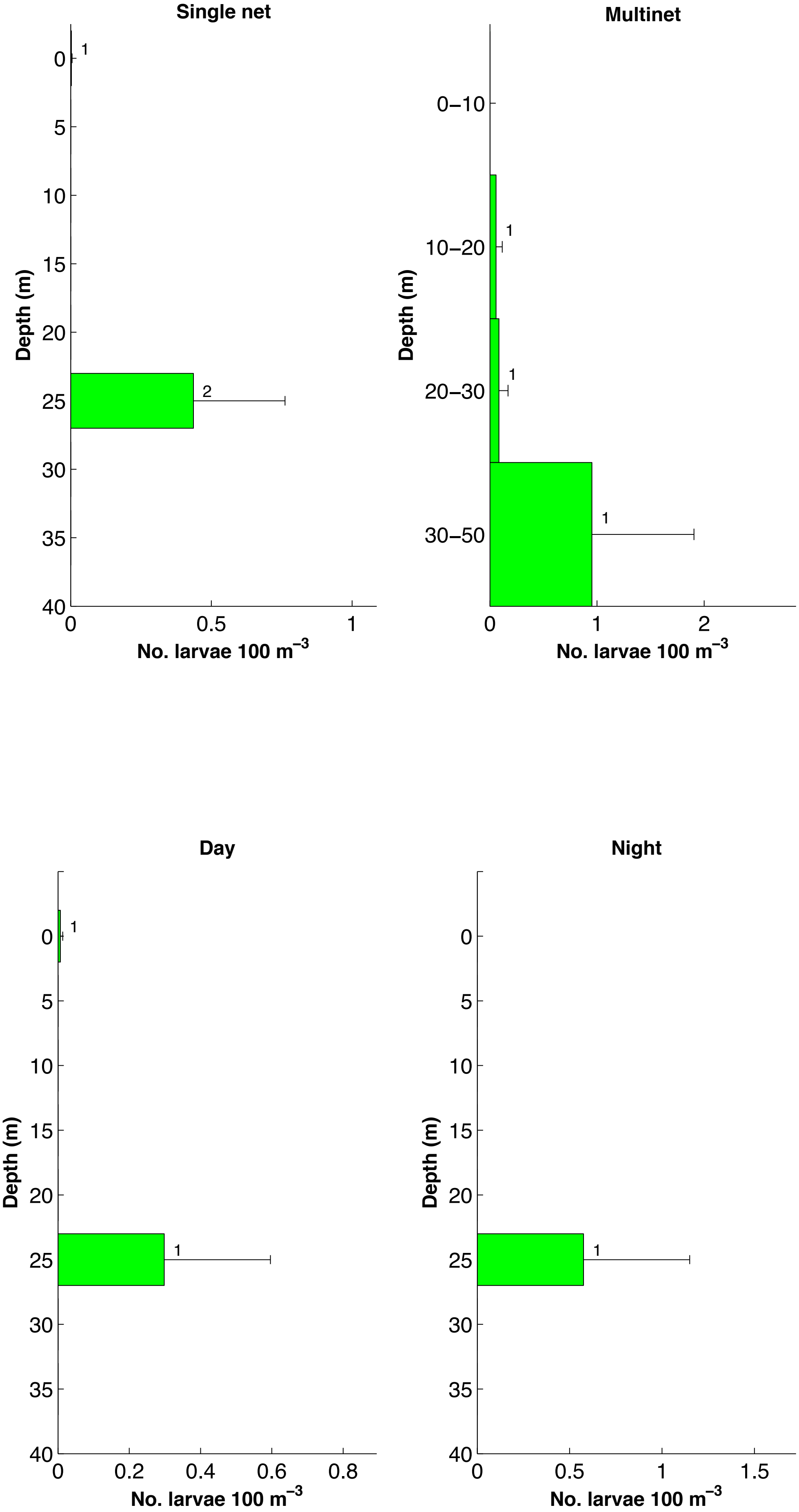
Aphia minuta


Single net

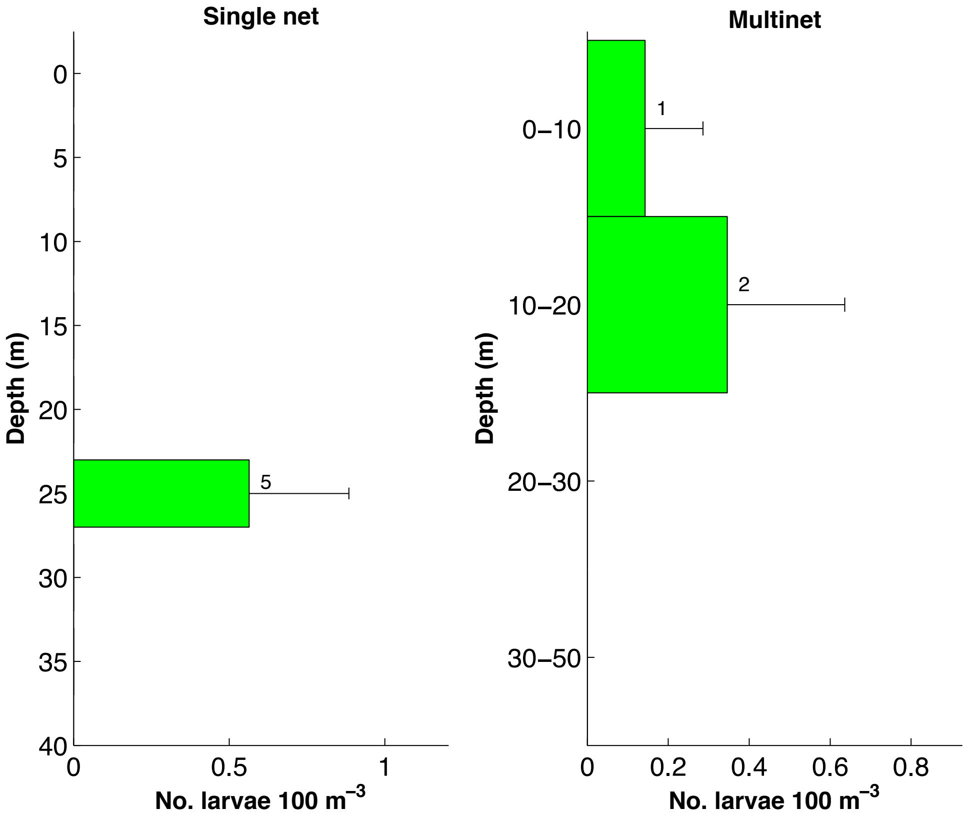

Night

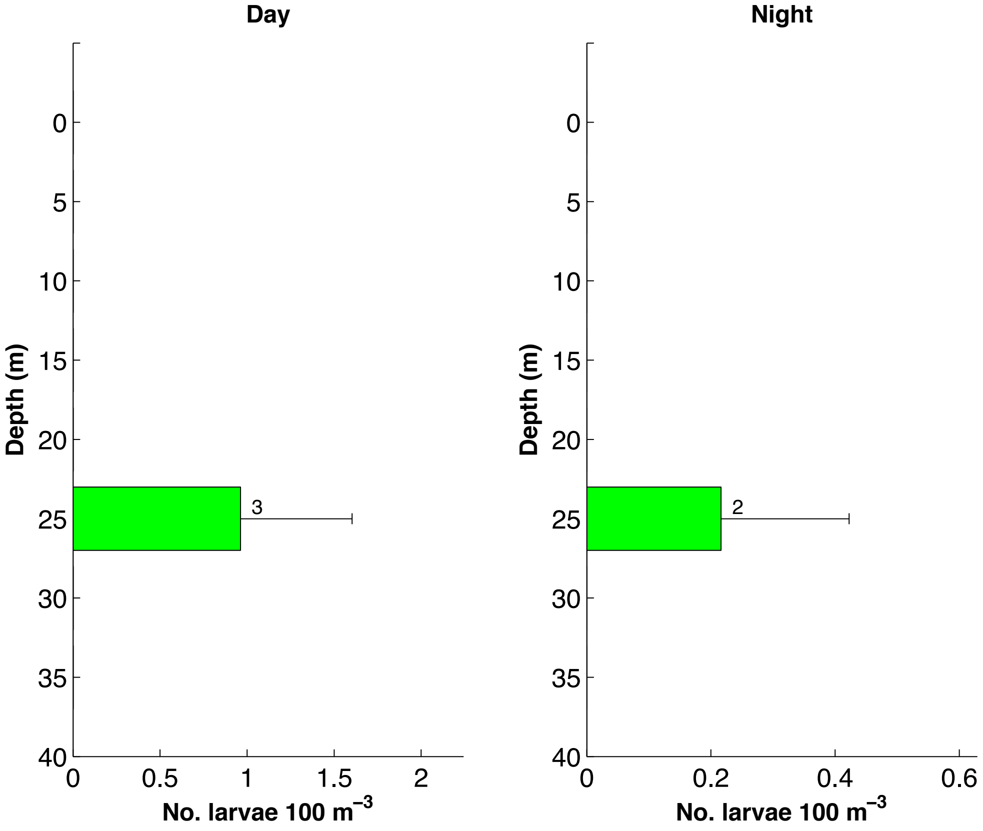
153

Crystallogobius nilssonii



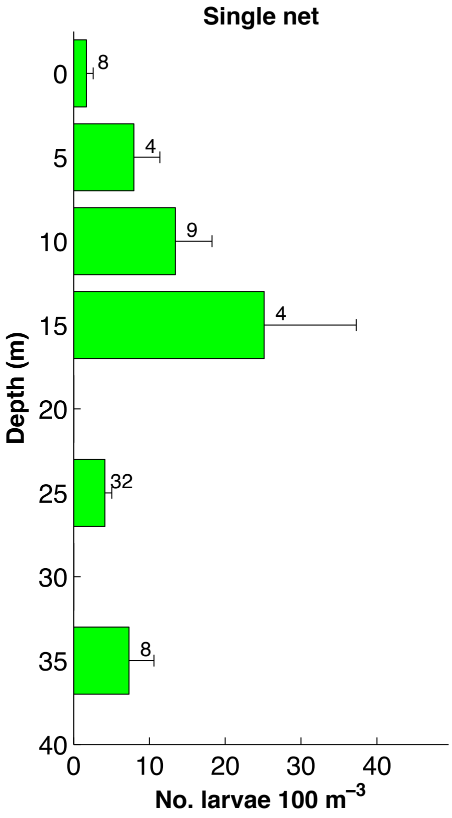
Pomatoschistus sp.

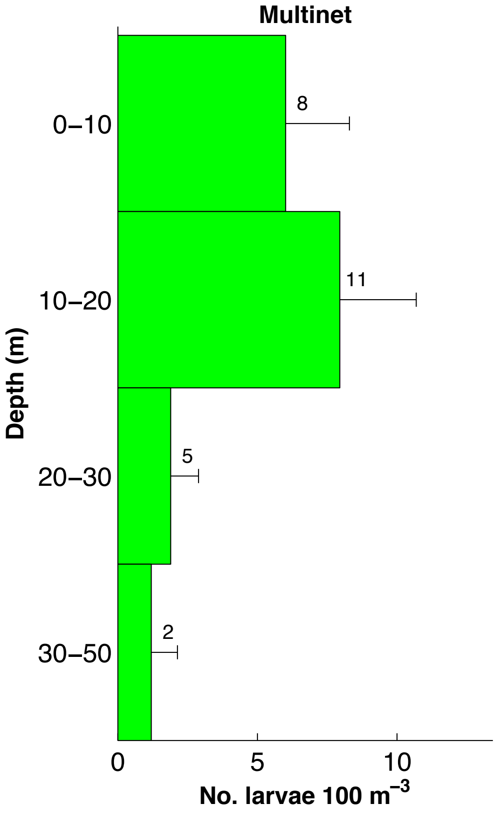


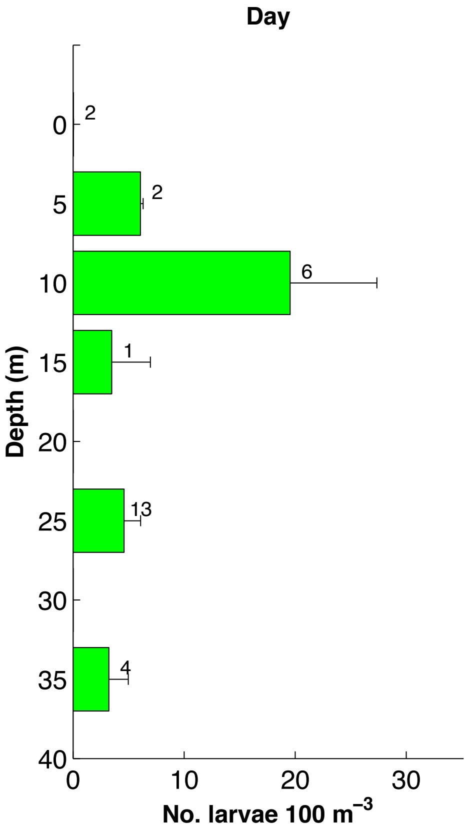


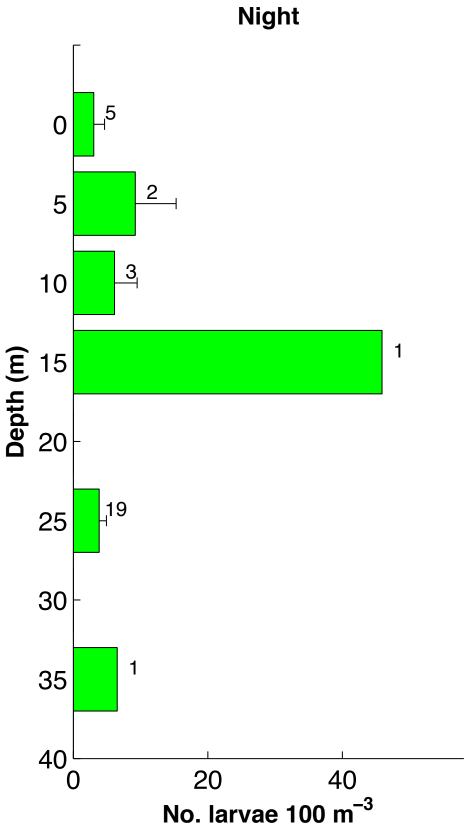
155

Gobidae

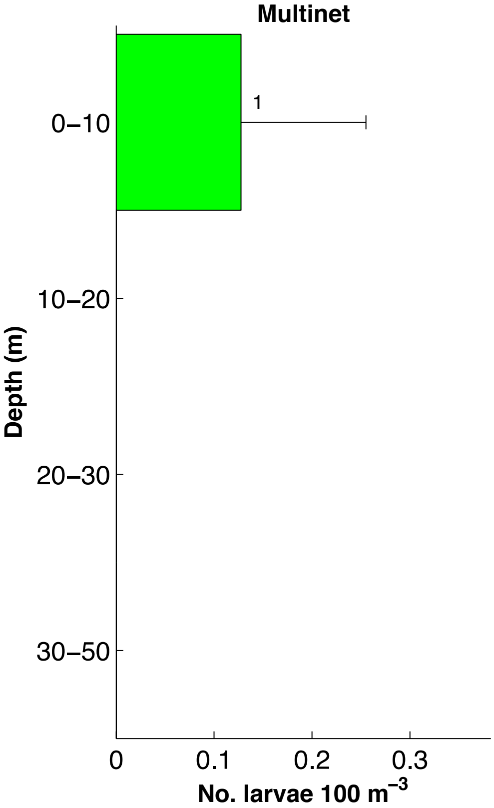

Single net
Depth (m)
0
5
10
15
20
25
30
35
40
8
4
9
4
32
8
0
10
20
30
40
No. larvae 100 m^{-3}


Multinet
Depth (m)
0–10
10–20
20–30
30–50
8
11
5
2
0
5
10
No. larvae 100 m^{-3}


Day
Depth (m)
0
5
10
15
20
25
30
35
40
2
2
6
1
13
4
0
10
20
30
No. larvae 100 m^{-3}

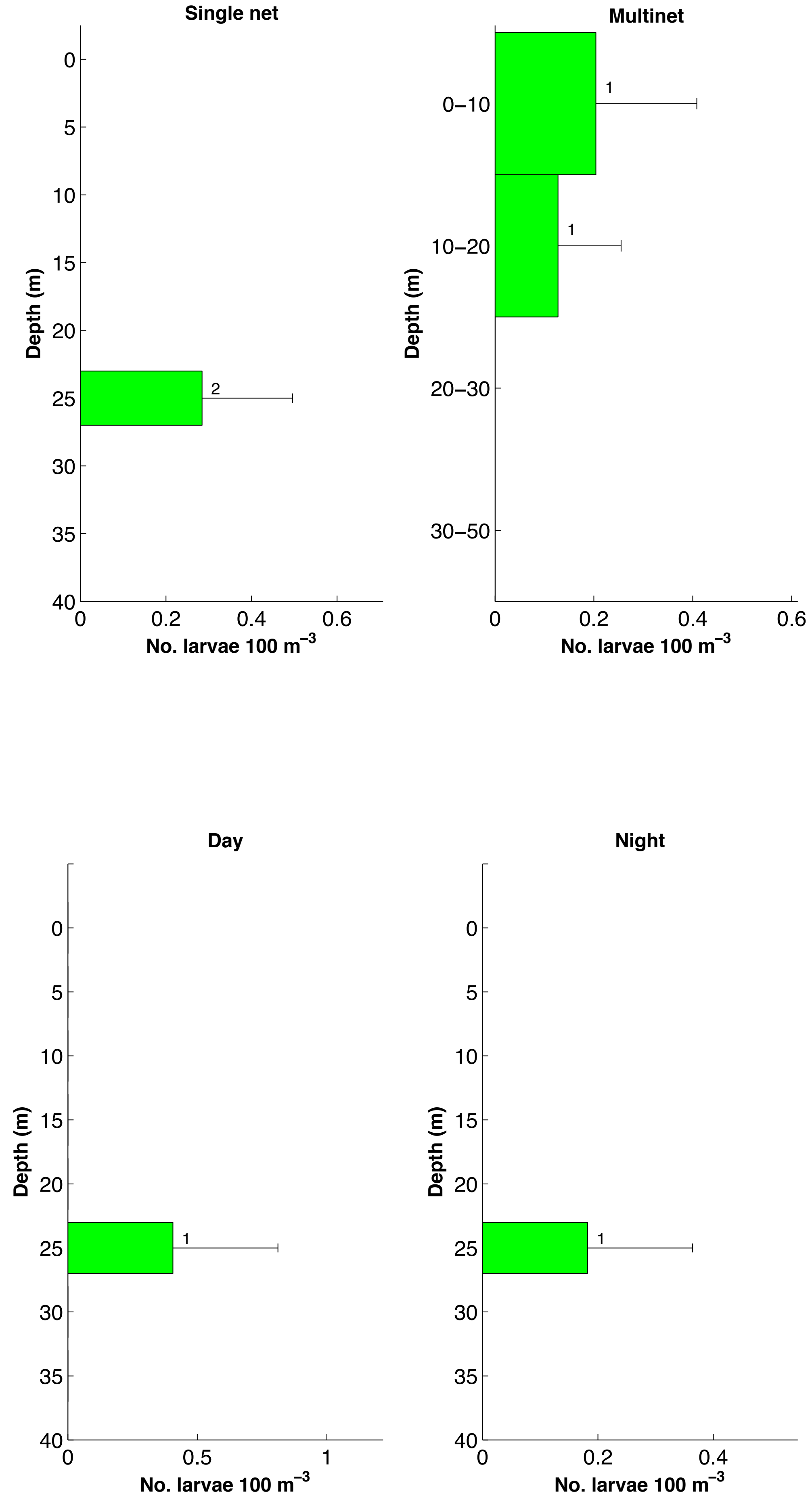

Night
Depth (m)
0
5
10
15
20
25
30
35
40
5
2
3
1
19
1
0
20
40
No. larvae 100 m^{-3}

Pholis gunellus

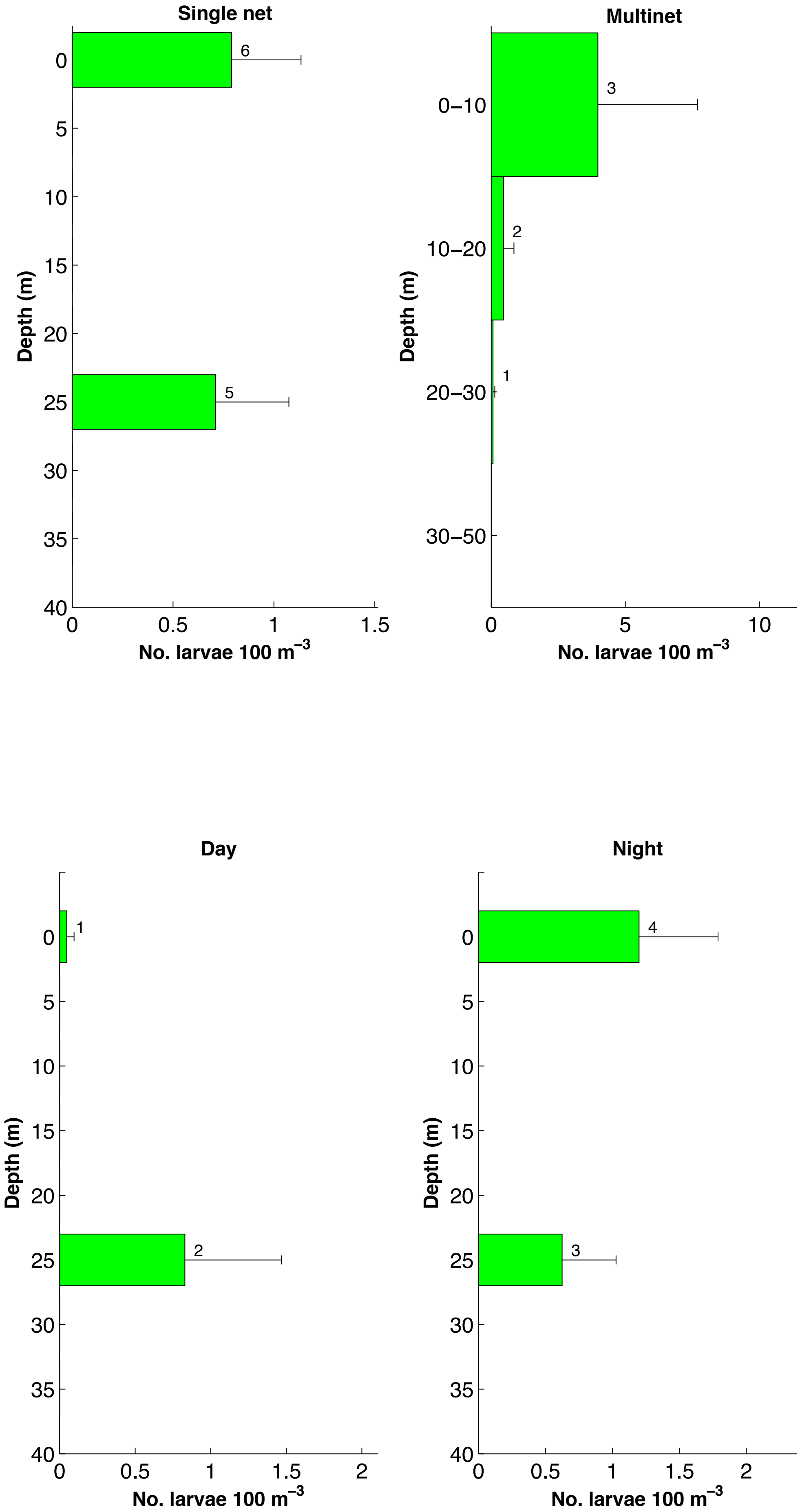


157

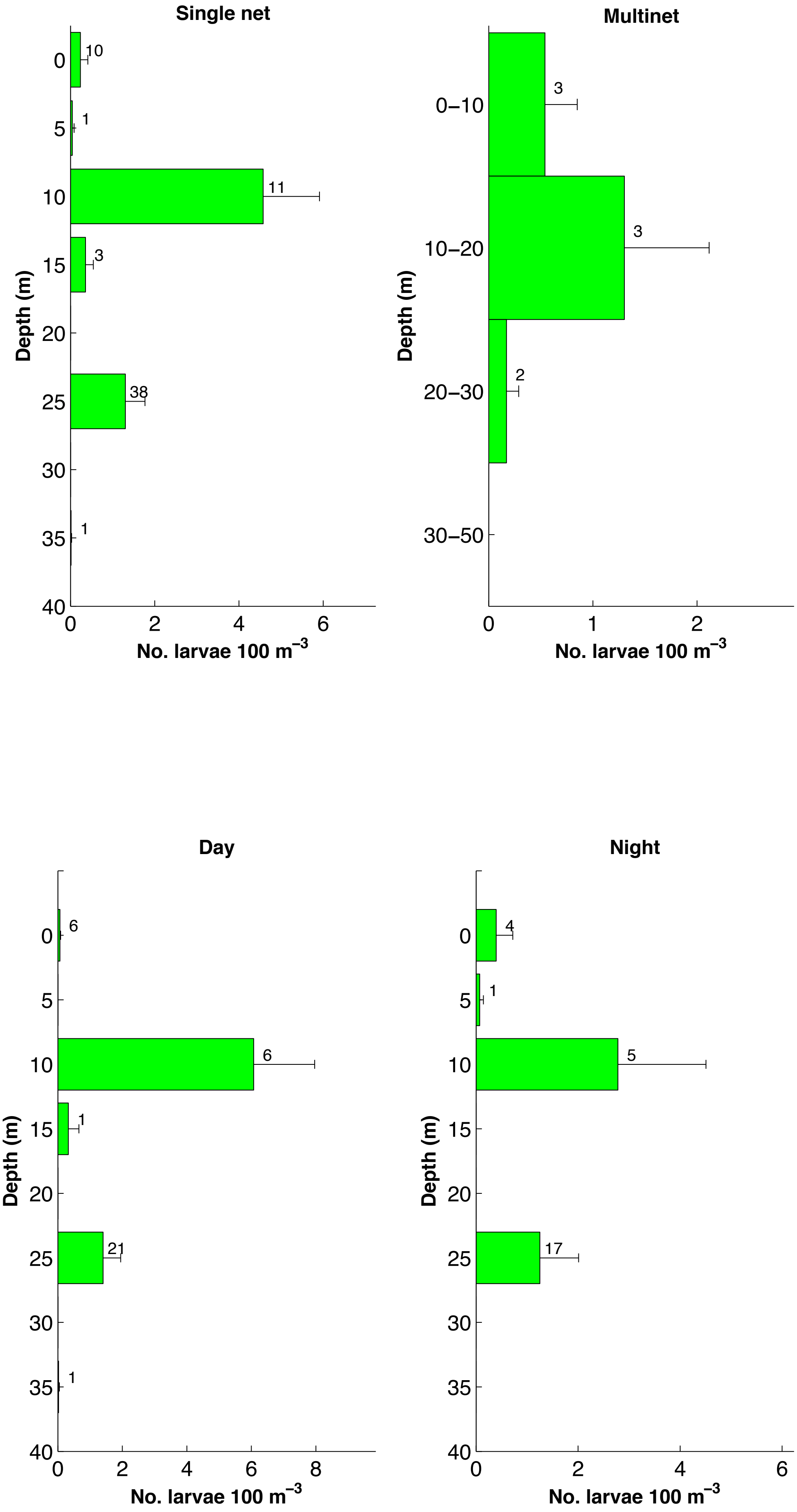
Scomber sp.



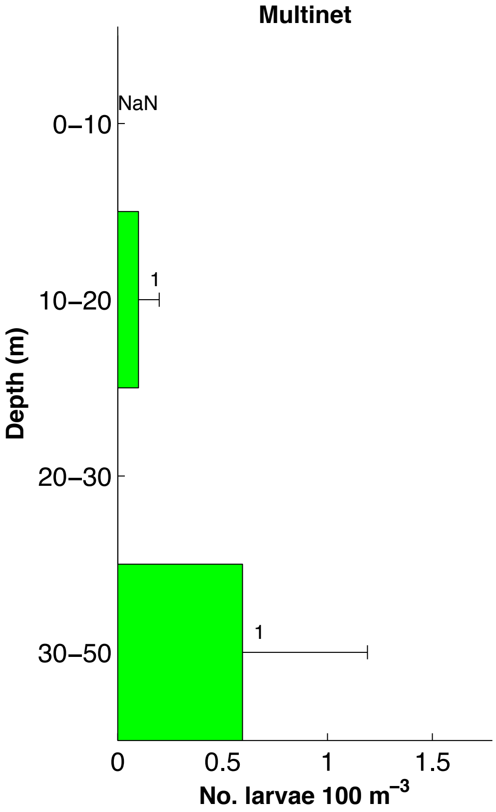
Trachinus sp.



Arnoglossus laterna

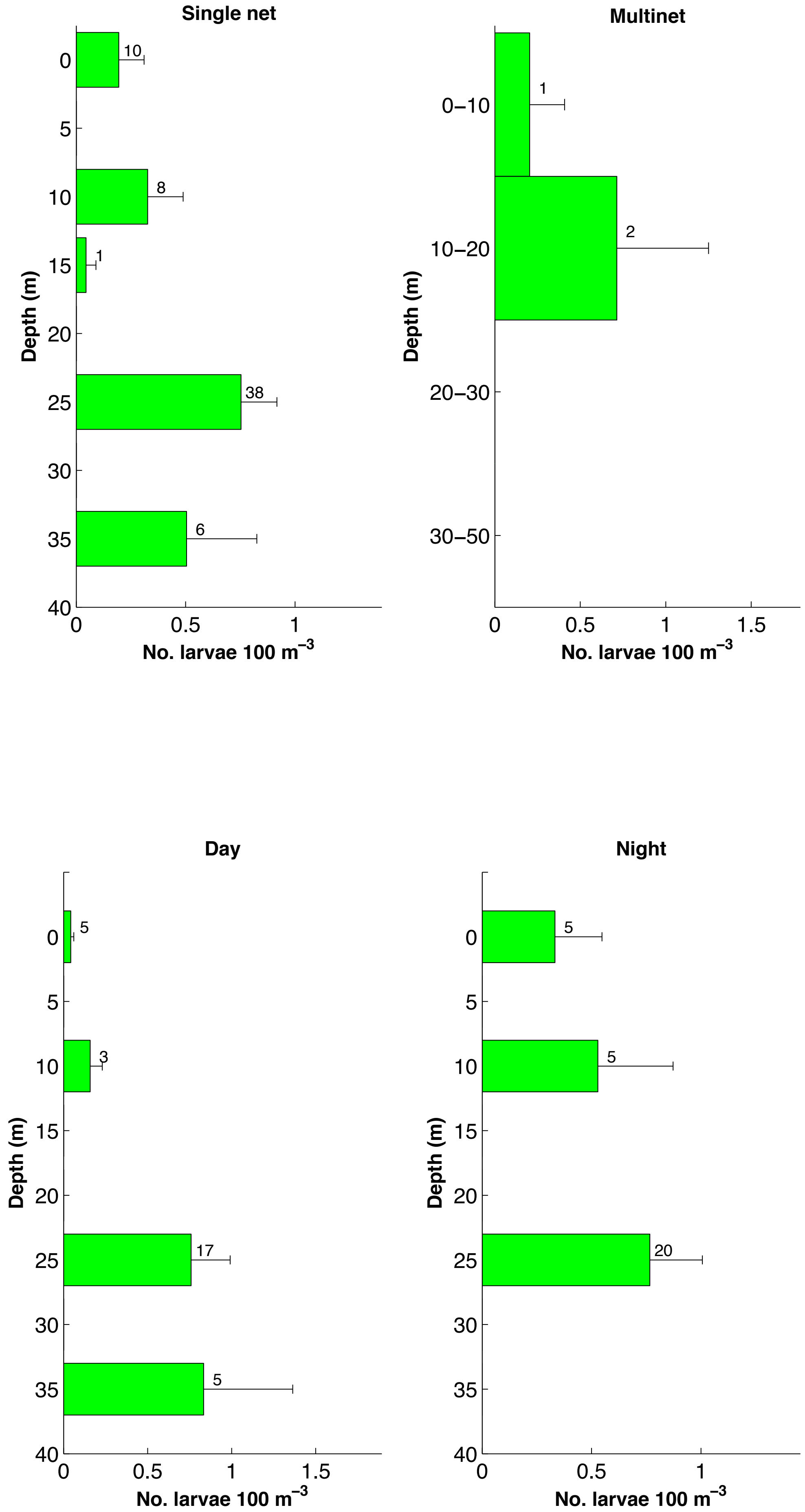


Pleuronectidae

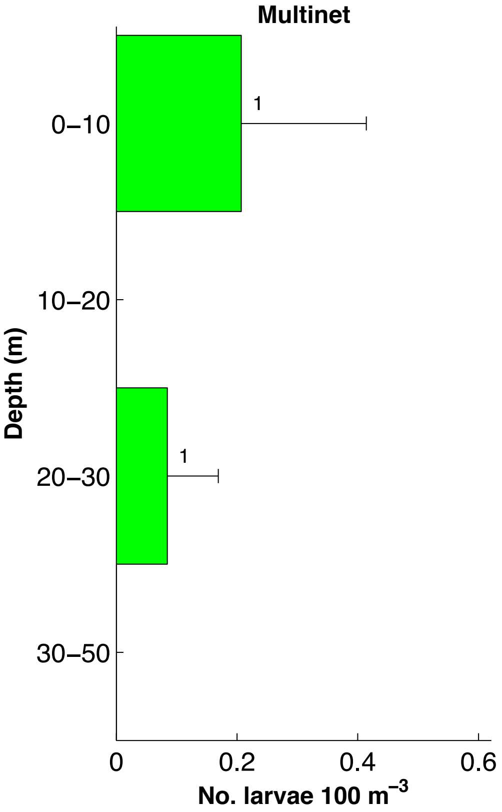


161

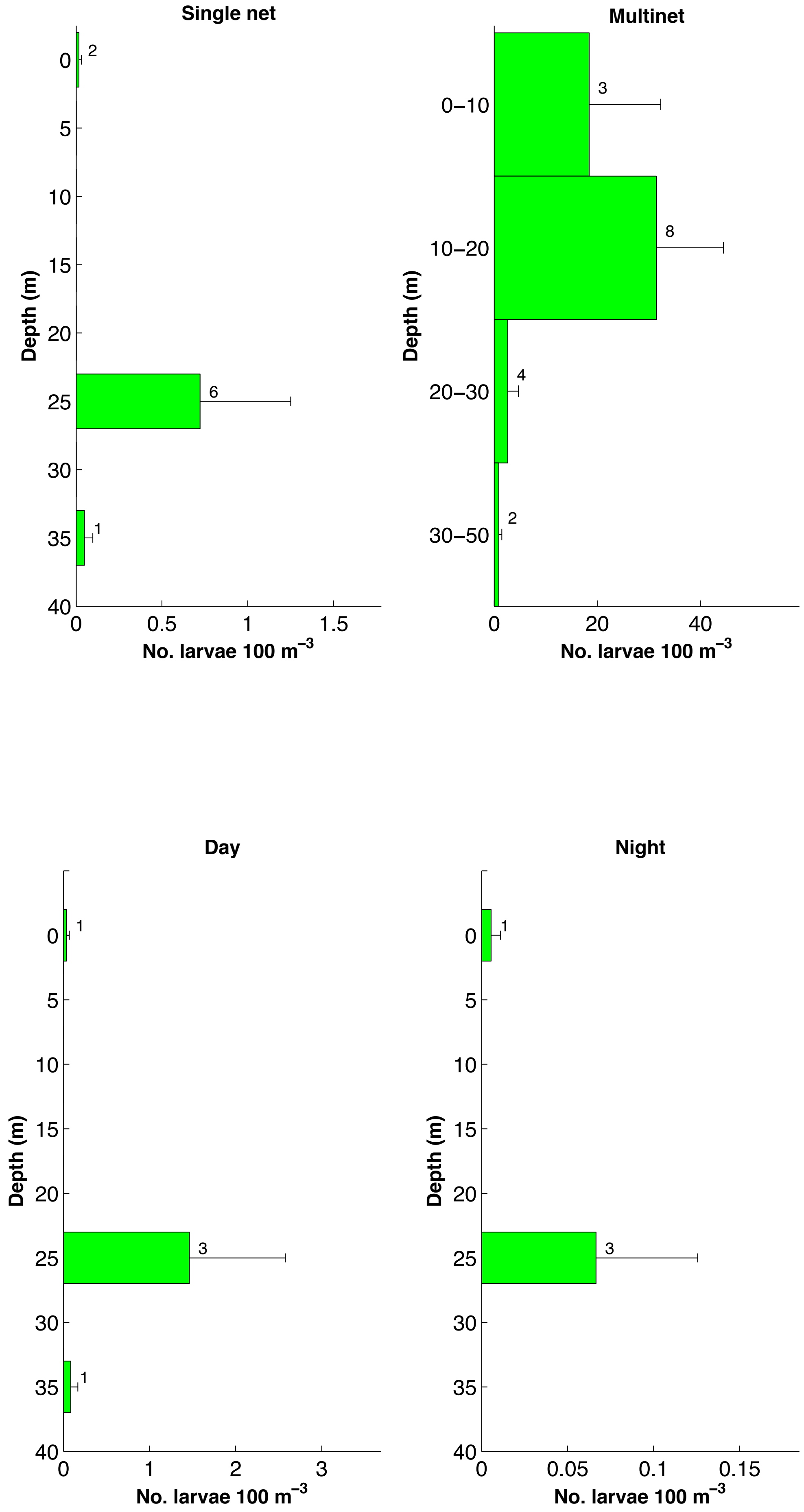
Buglossidium luteum



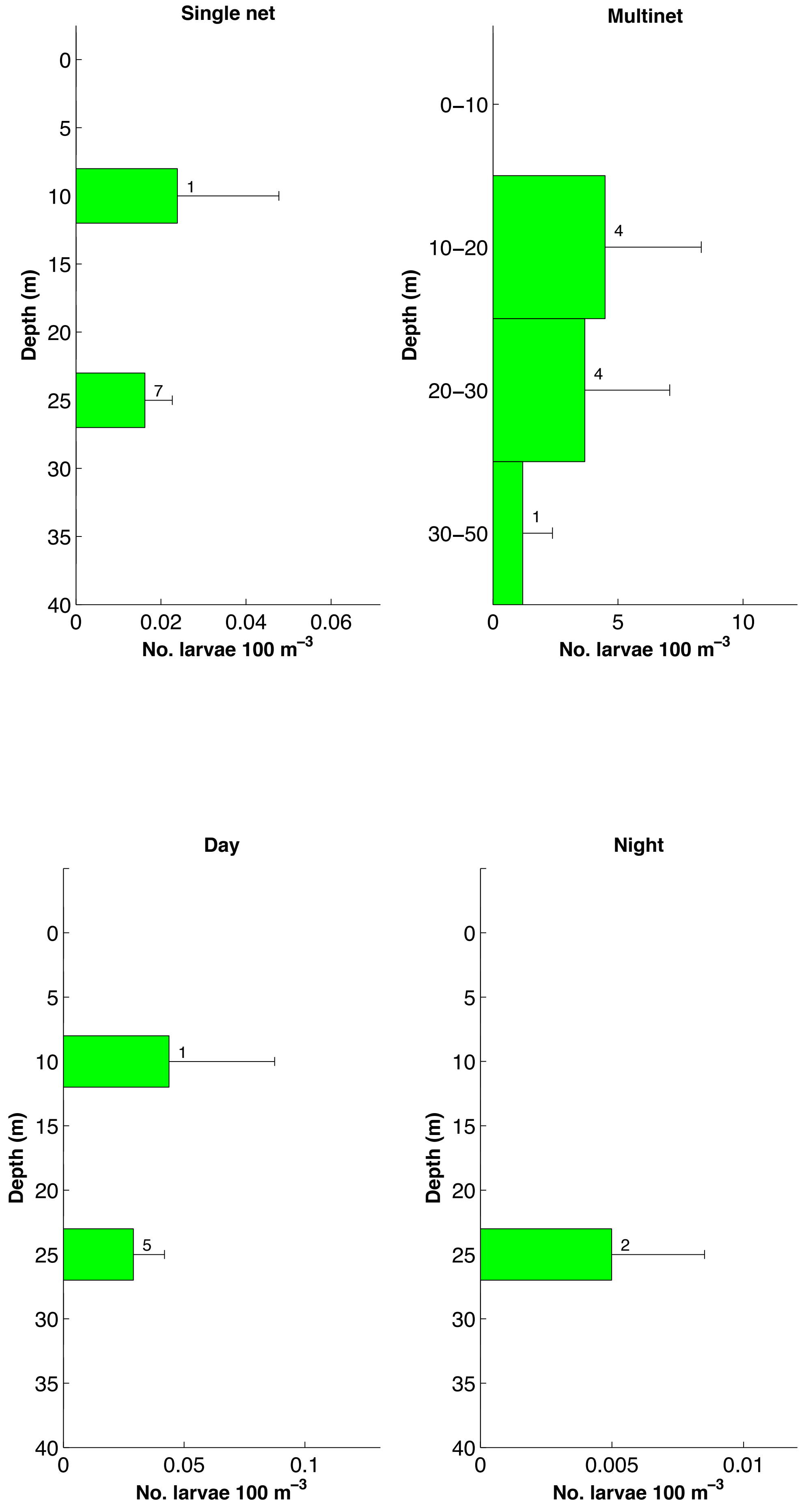
Hippoglossoides platessoides



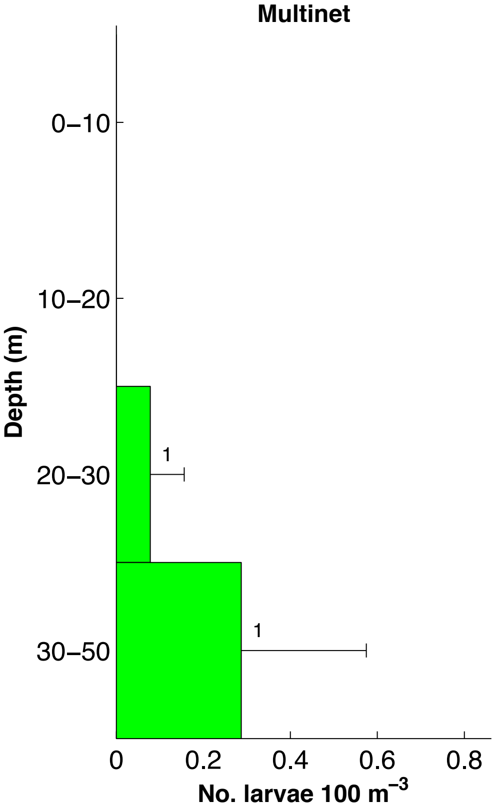
Limanda limanda 5



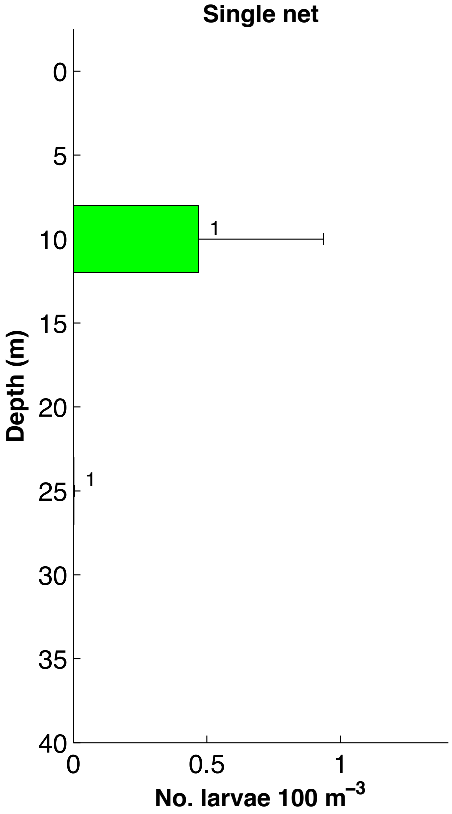
Limanda limanda> 5

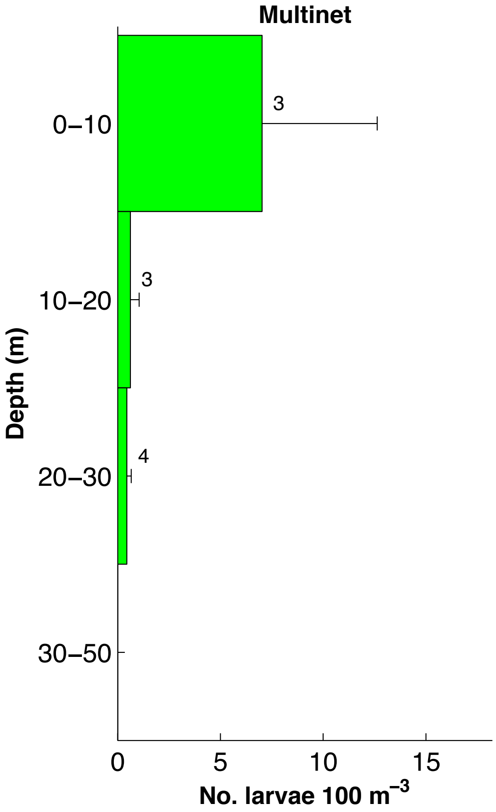


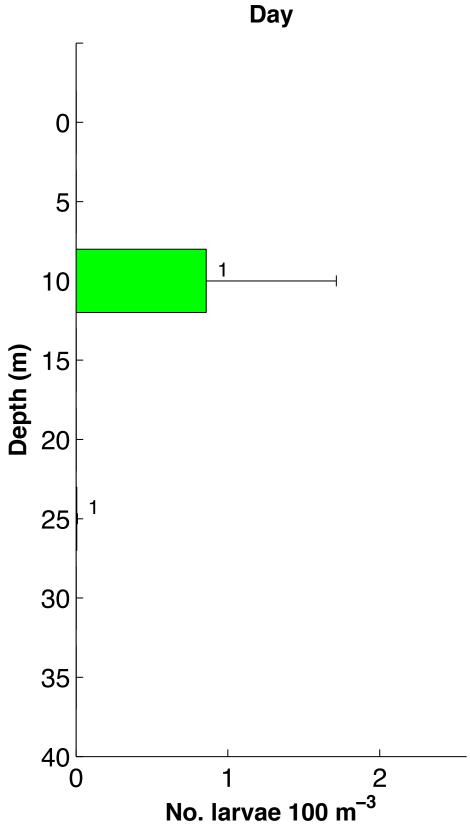
Microstomus kitt



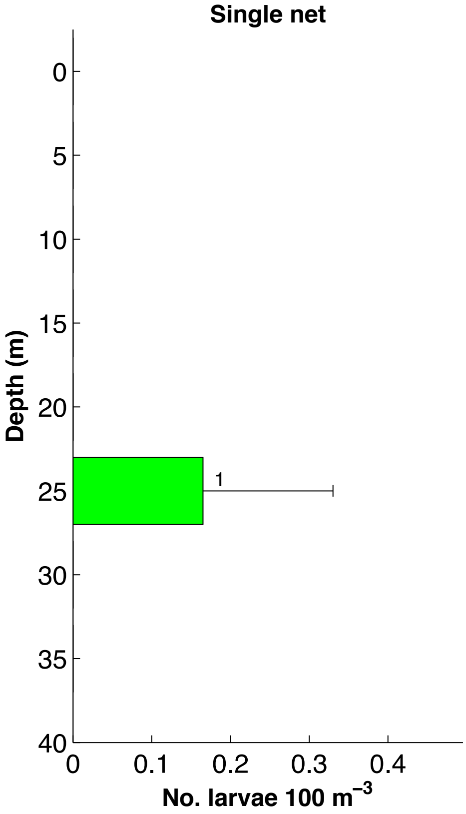
Platichtys flesus

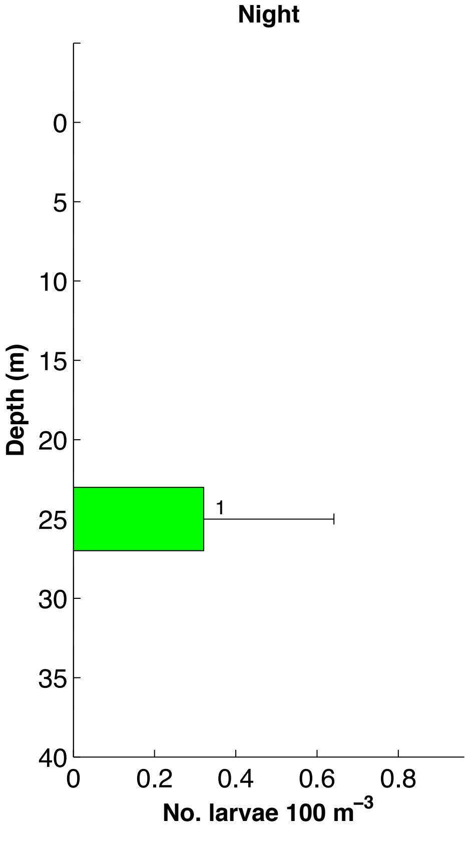






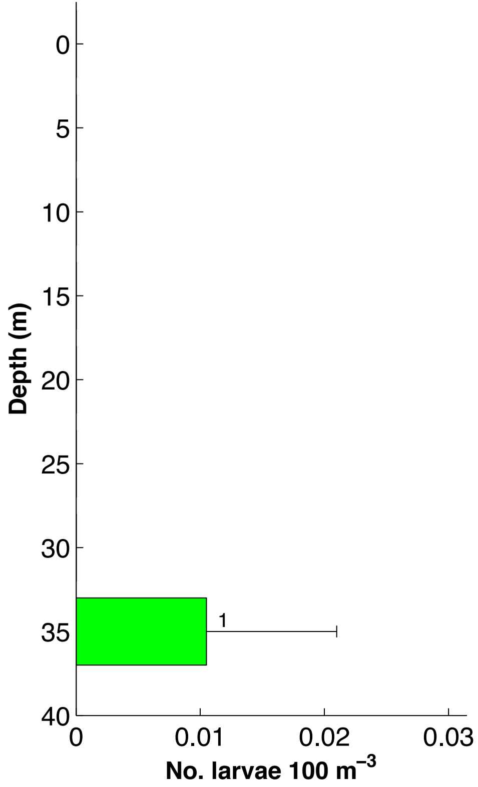
Pleuronectes platessa



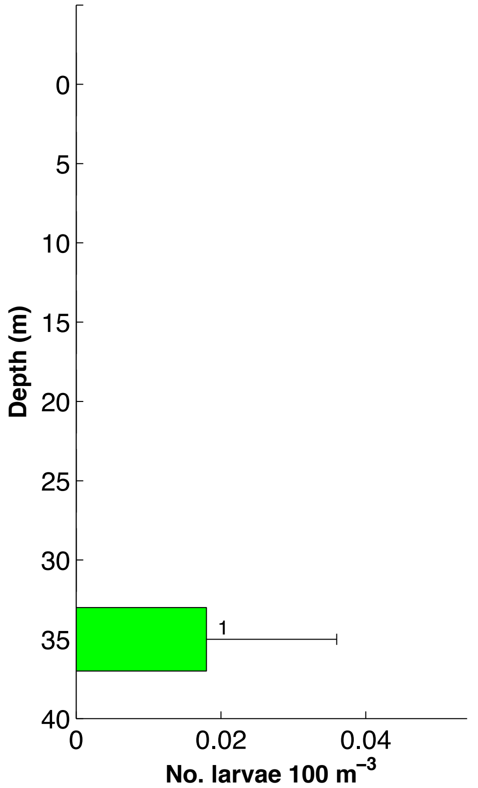


Phrynorhombus norvegicus

Single net

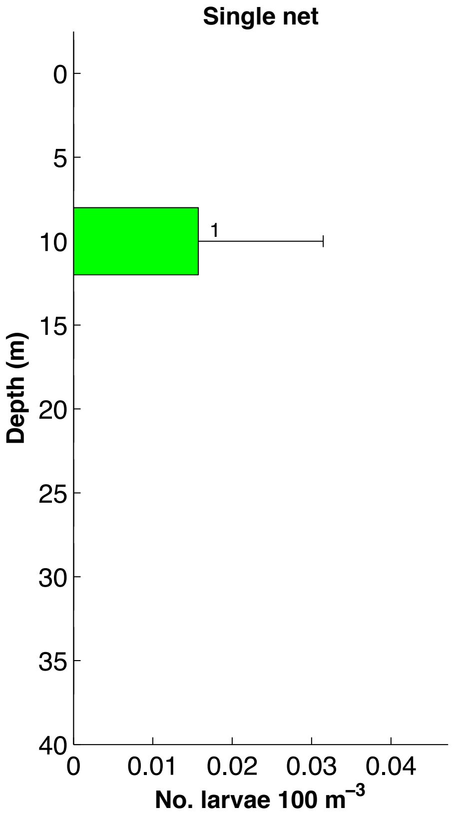


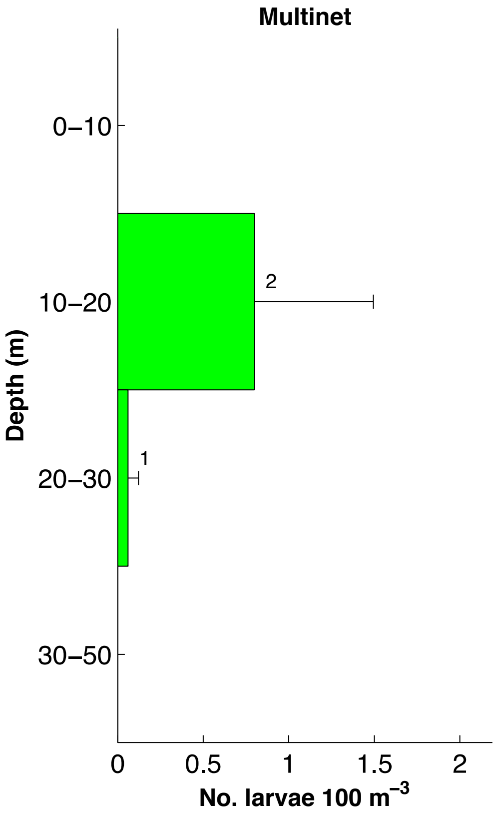
Day

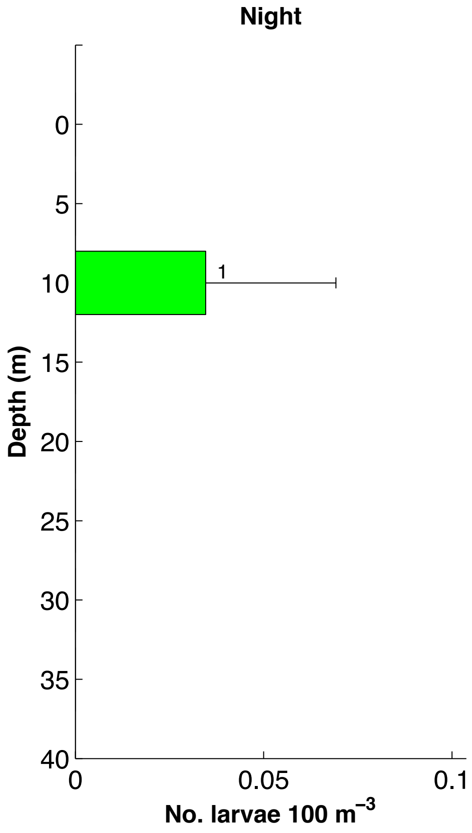


169

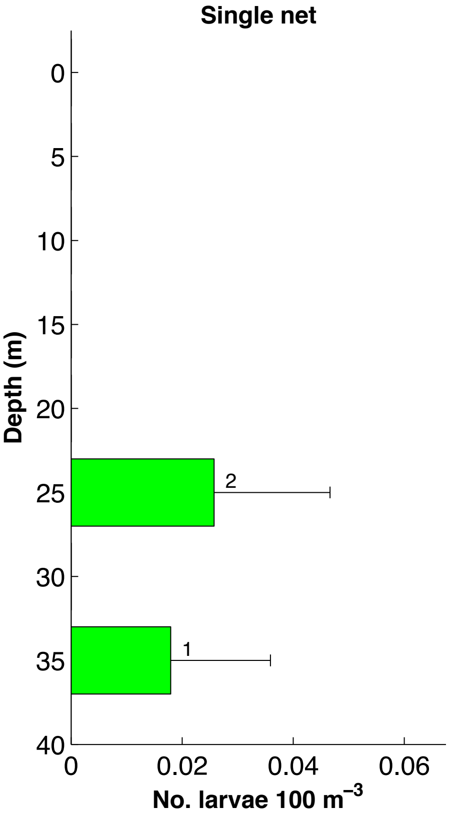
Psetta/Scophtalmus sp.

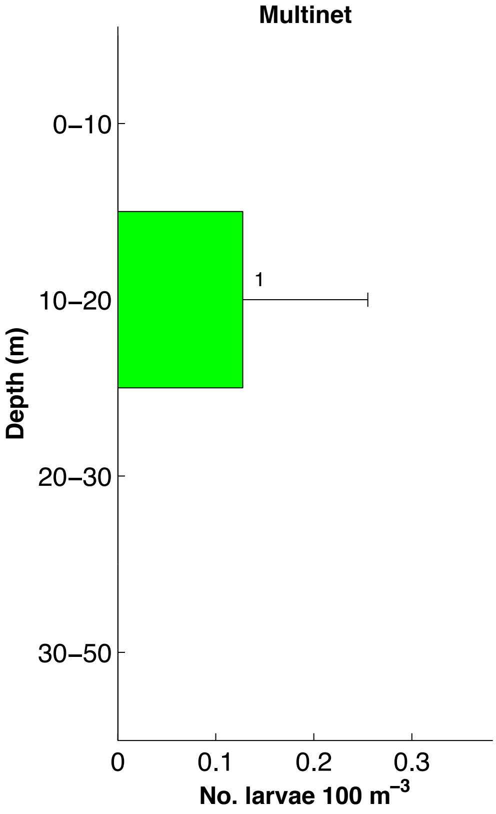


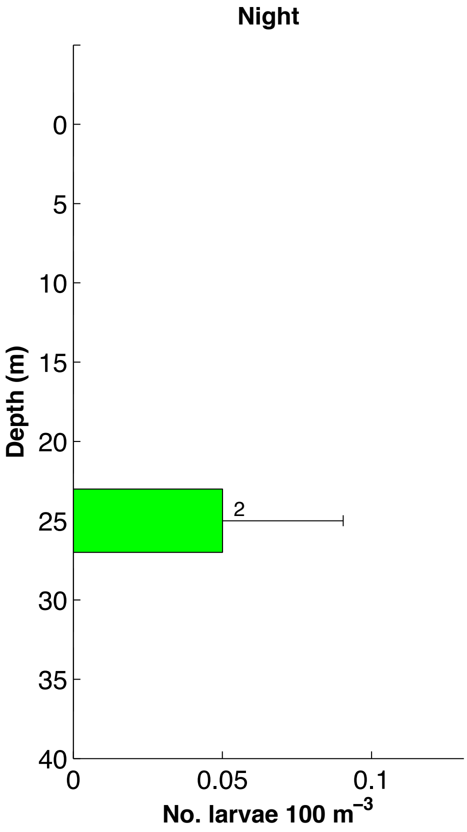




Zeugopterus punctatus

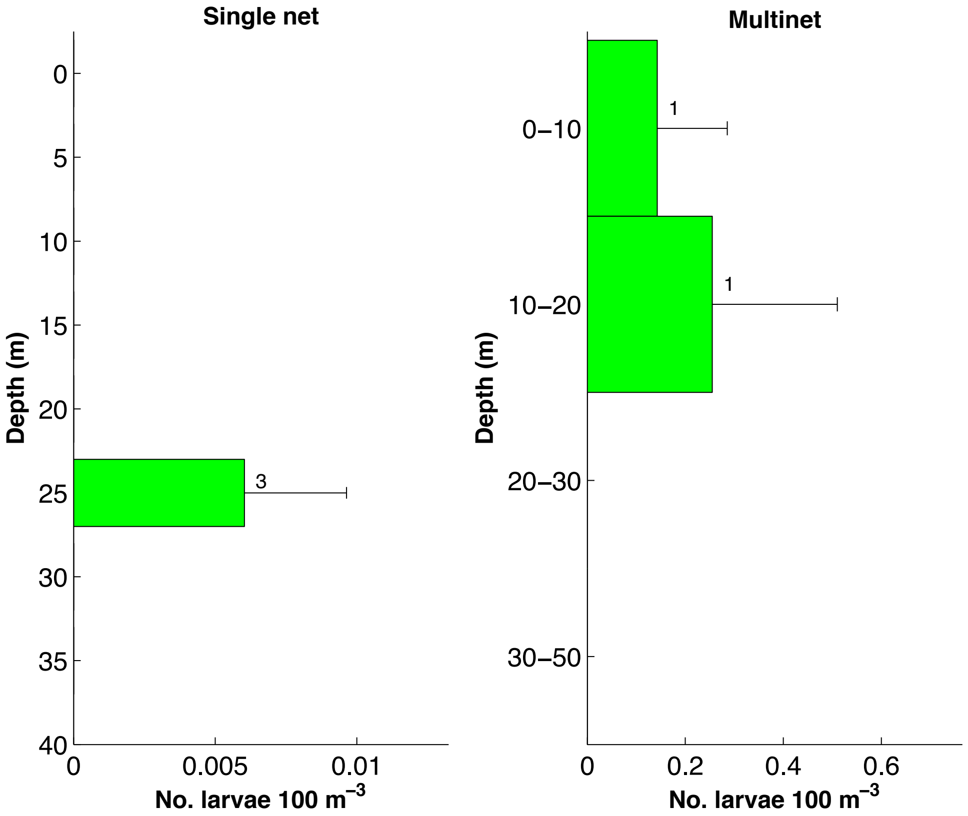


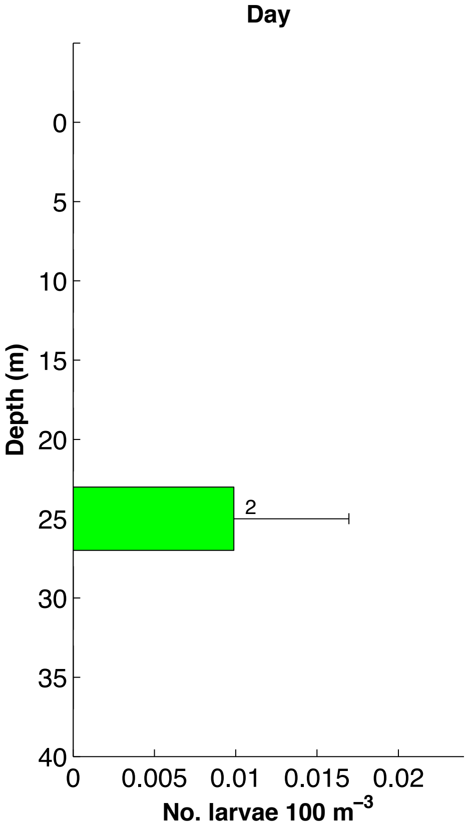




171

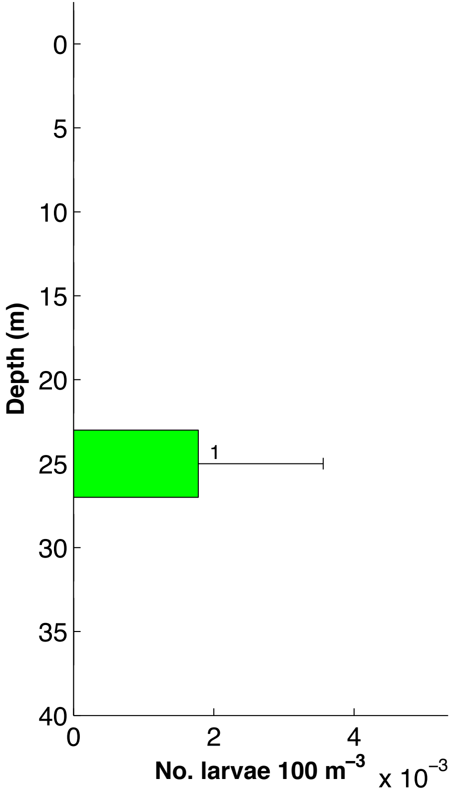
Solea sp.


Single net
Depth (m)
0
5
10
15
20
25
30
35
40
3
0
0.005
0.01
No. larvae 100 m^{-3}
Multinet
Depth (m)
0–10
10–20
20–30
30–50
1
1
0
0.2
0.4
0.6
No. larvae 100 m^{-3}

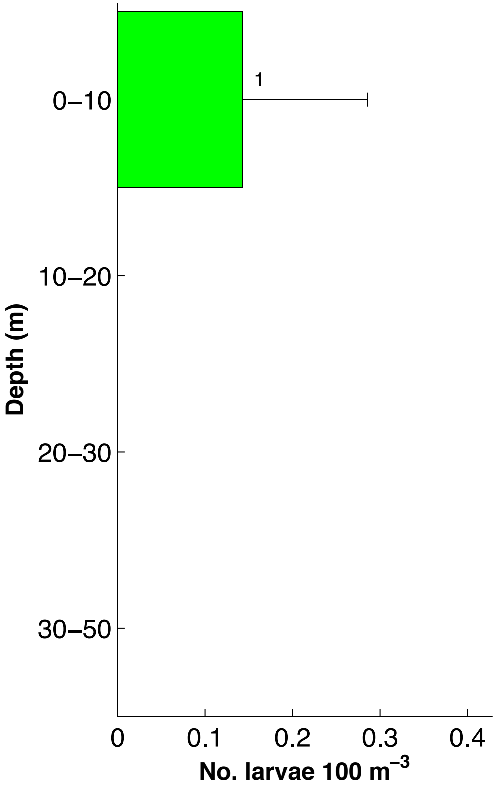

Day
Depth (m)
0
5
10
15
20
25
30
35
40
2
0
0.005
0.01
0.015
0.02
No. larvae 100 m^{-3}

Taurulus sp.

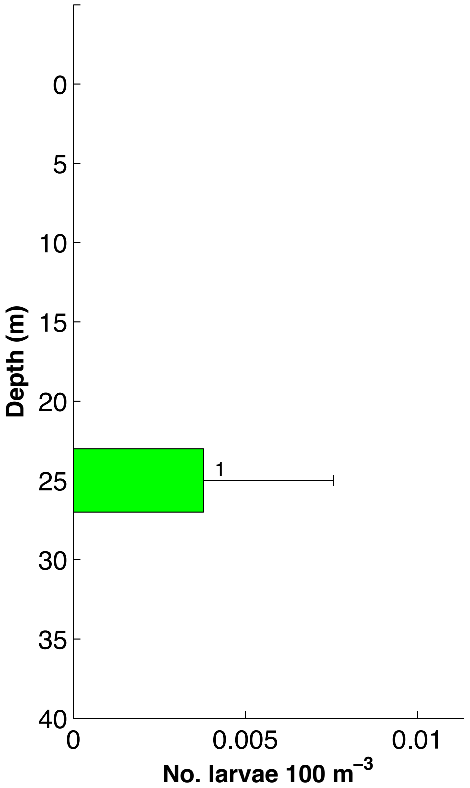
Single net



Multinet

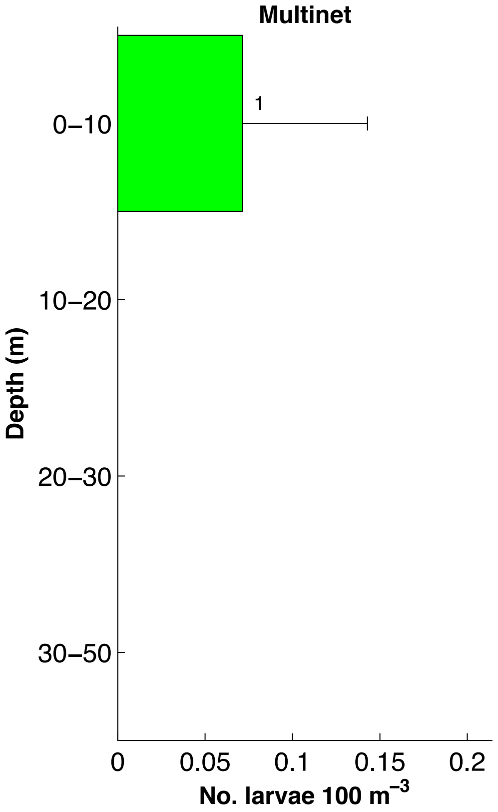


Day

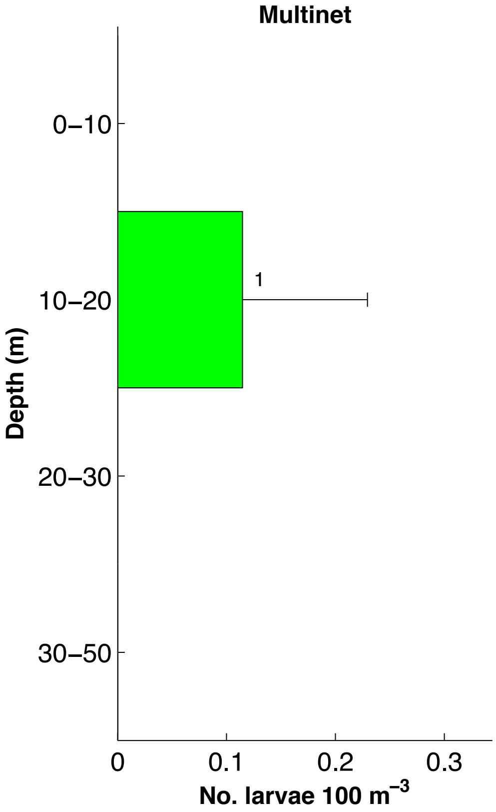


173

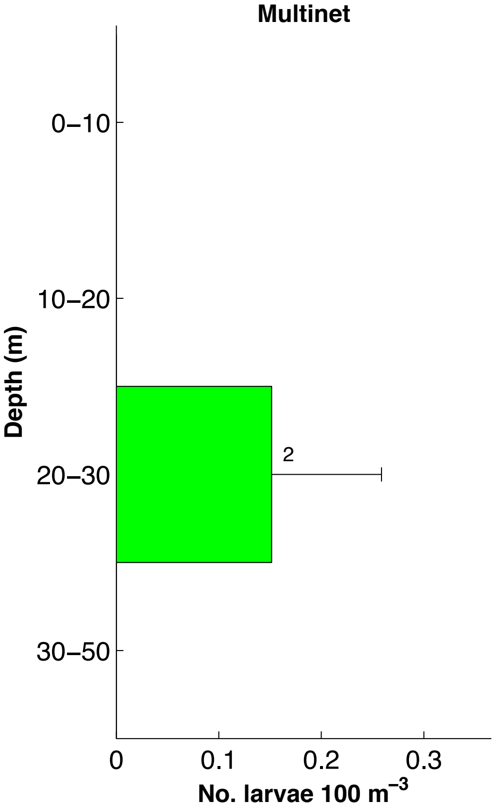
Triglidae



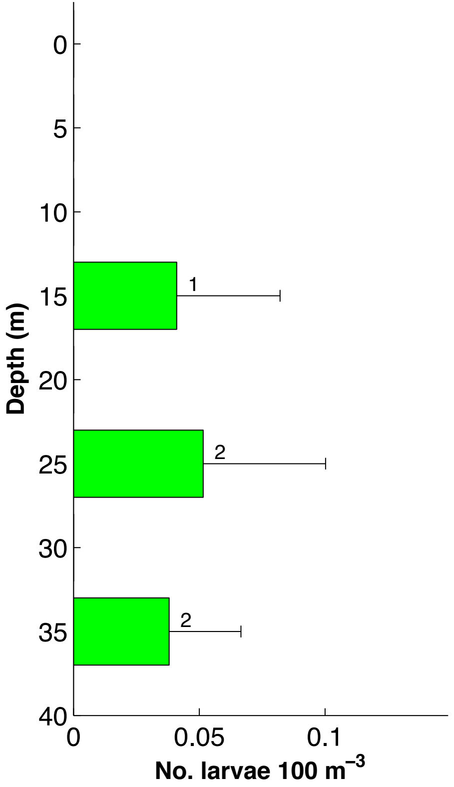
Cyclopterus lumpus

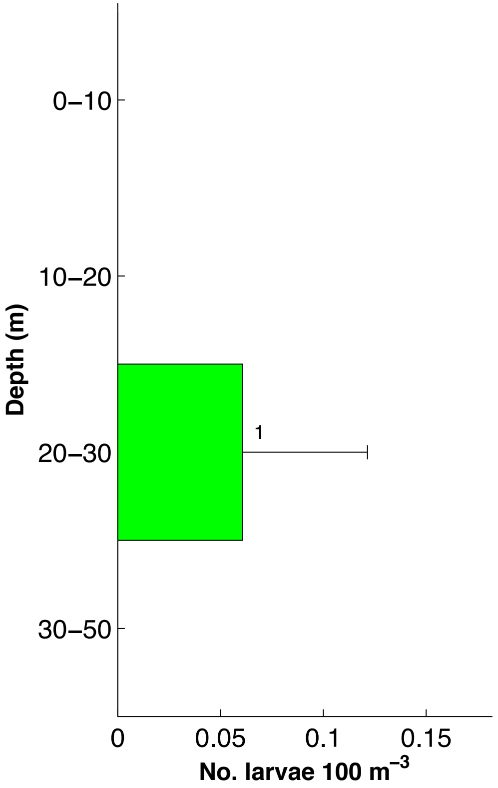


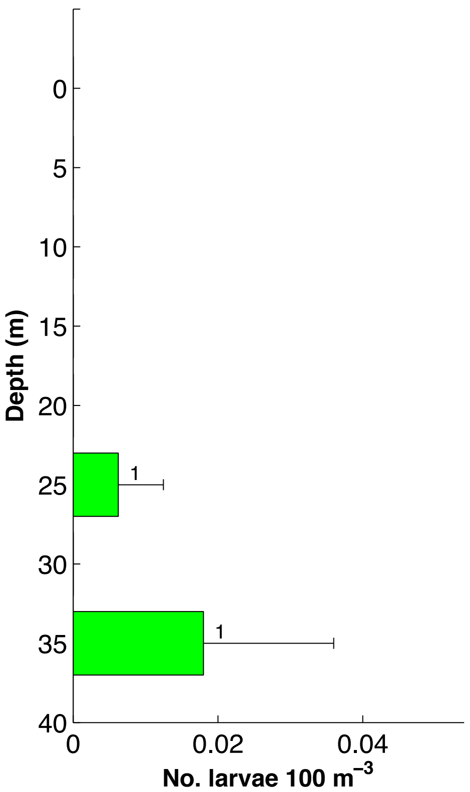
Liparis sp.

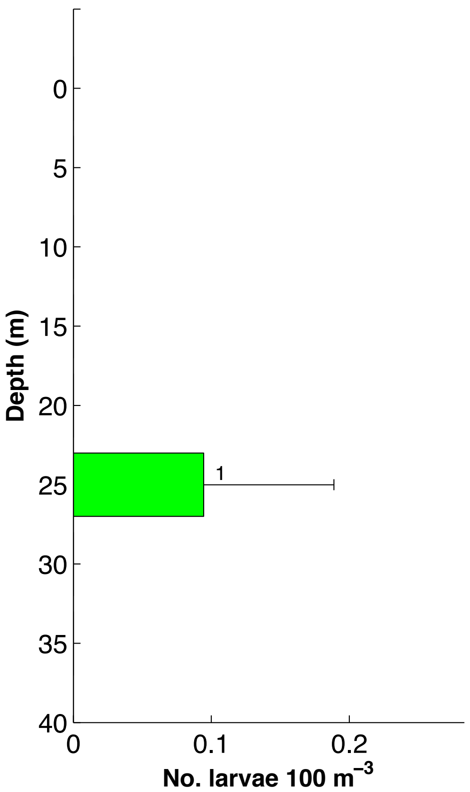

Multinet
Depth (m)
0–10
10–20
20–30
30–50
2
0
0.1
0.2
0.3
No. larvae 100 m^{-3}

Eutriglia gurnardus

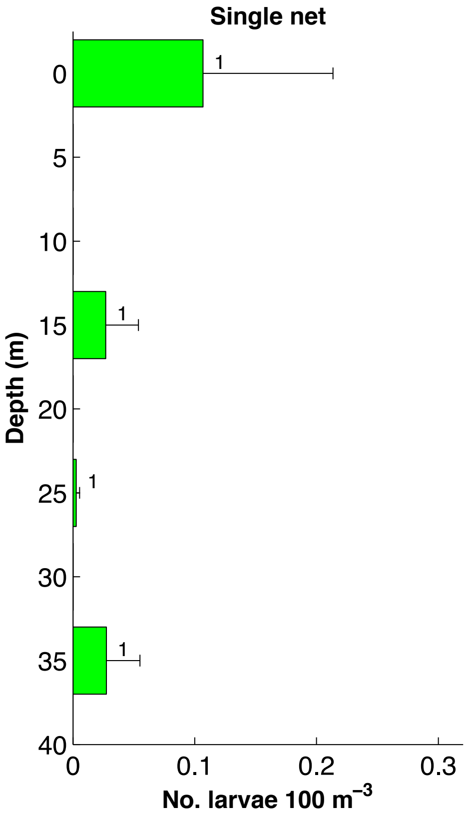

Single net

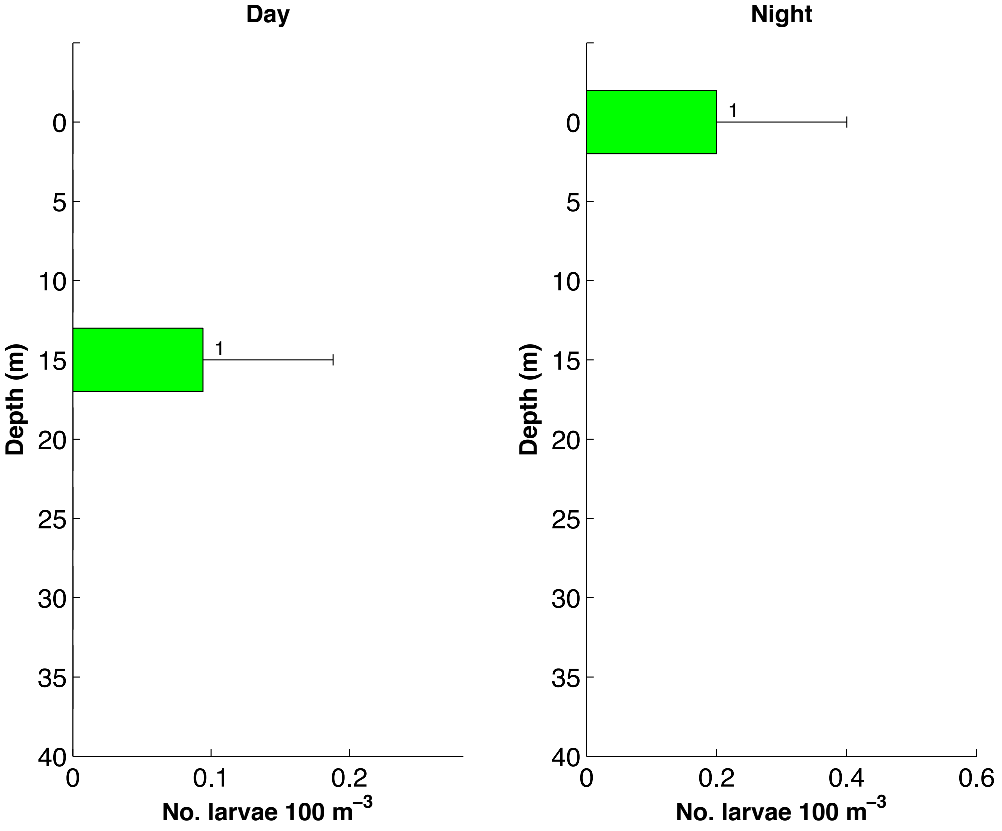

Multinet


Day

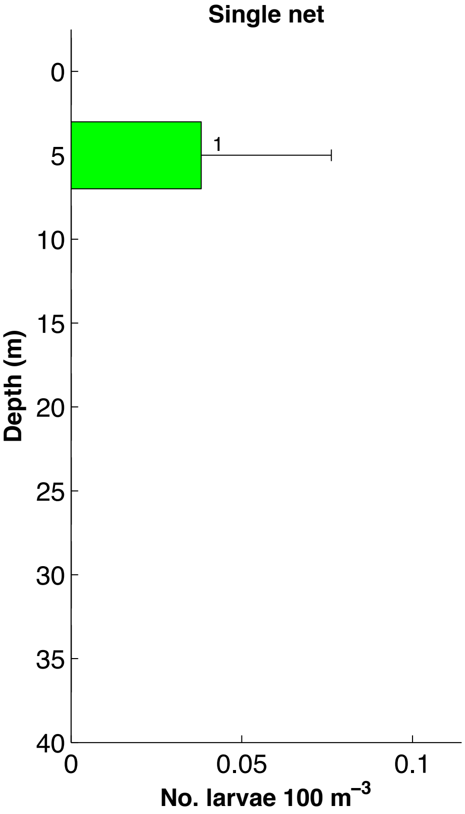

Night

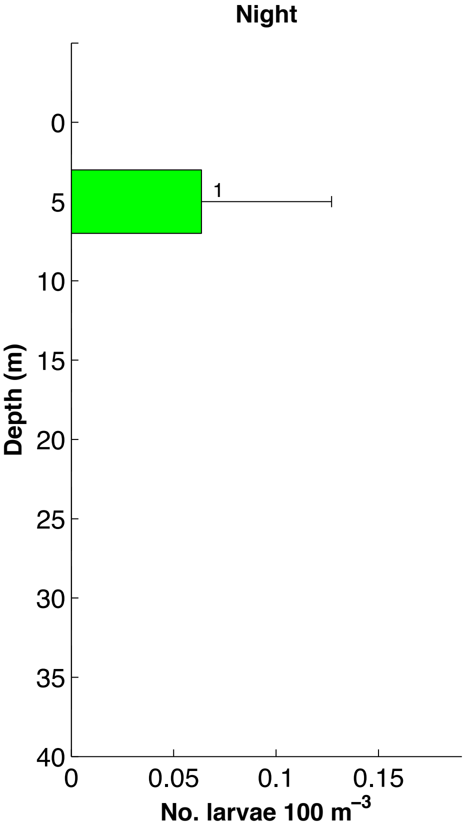
Entelurus aequoreus





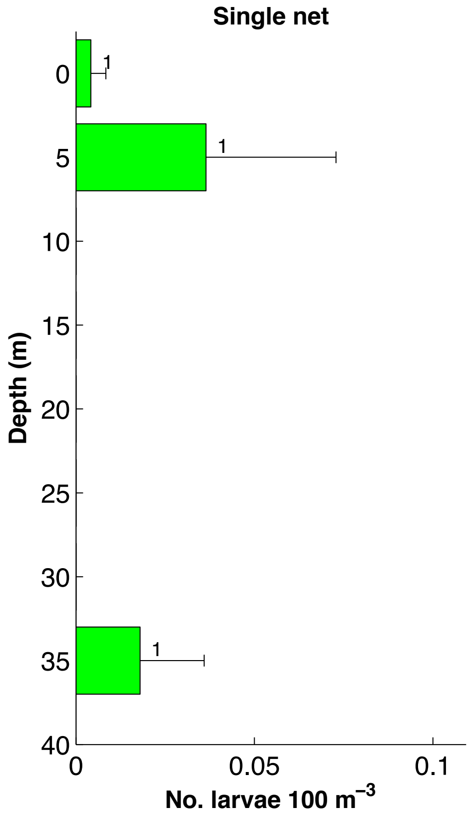
Nerophis sp.

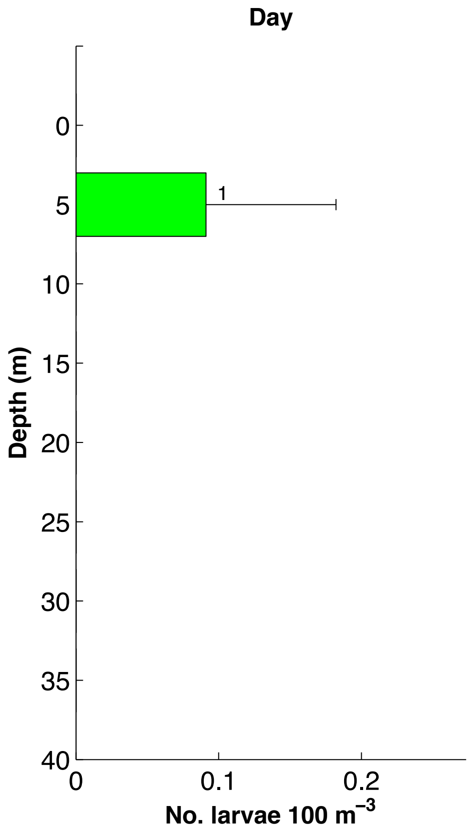

Single net
Depth (m)
0
5
10
15
20
25
30
35
40
1
0
0.05
0.1
No. larvae 100 m⁻³

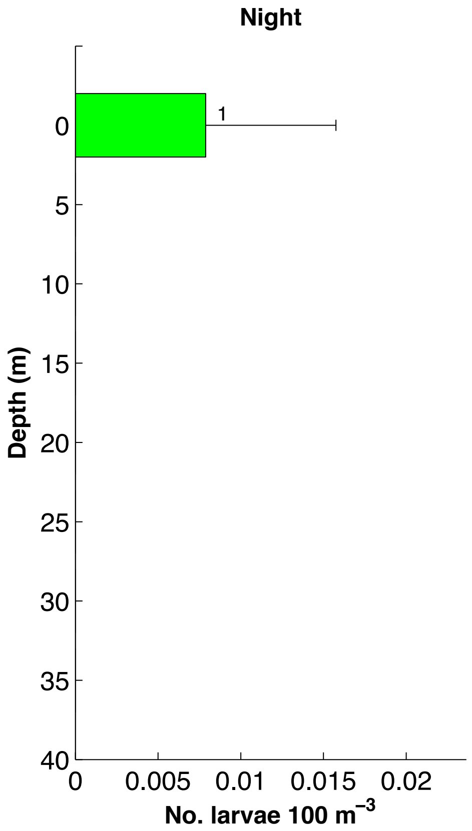

Night
Depth (m)
0
5
10
15
20
25
30
35
40
1
0
0.05
0.1
0.15
No. larvae 100 m⁻³

179

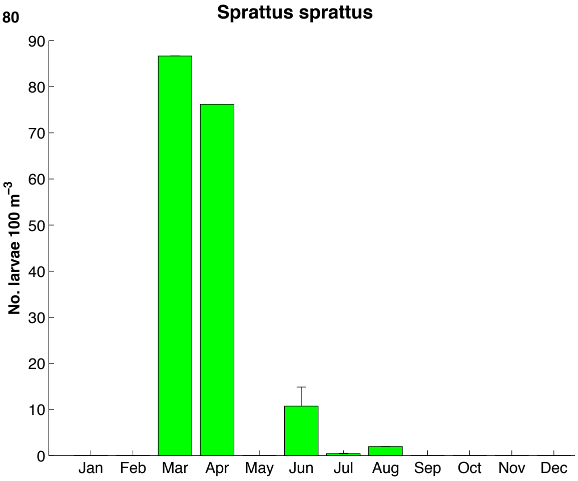
Syngnathus sp.





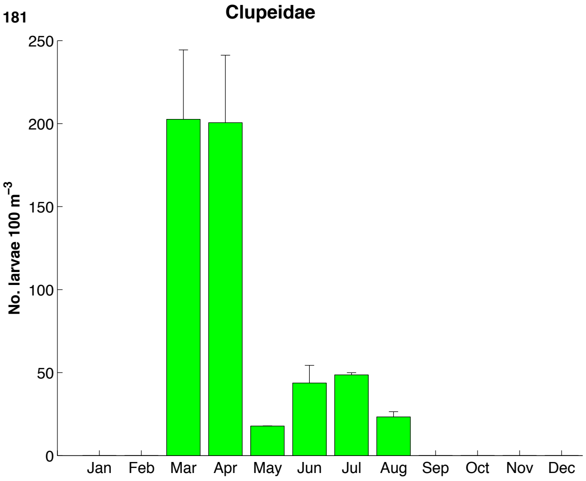


180



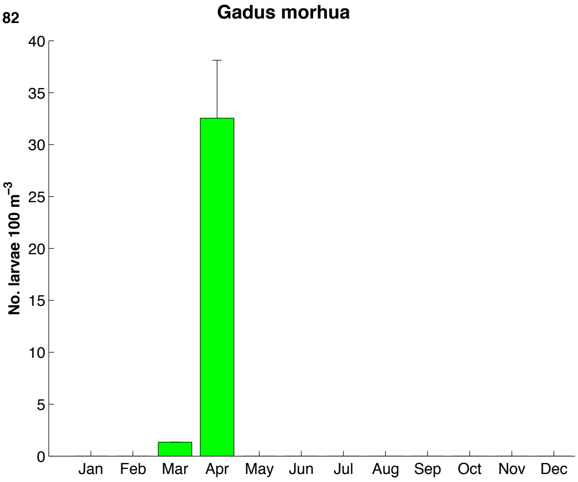
Sprattus sprattus

181



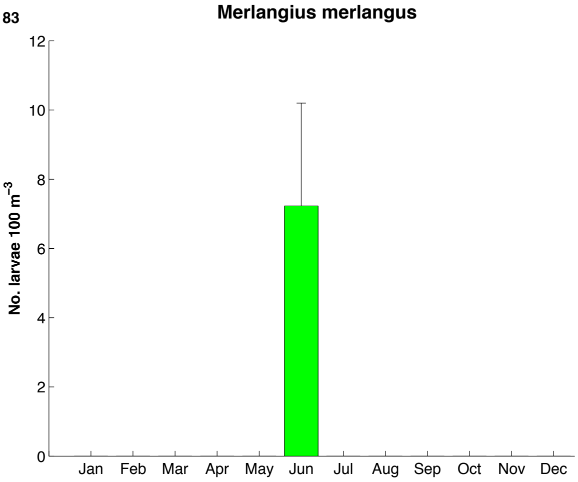
Clupeidae

182



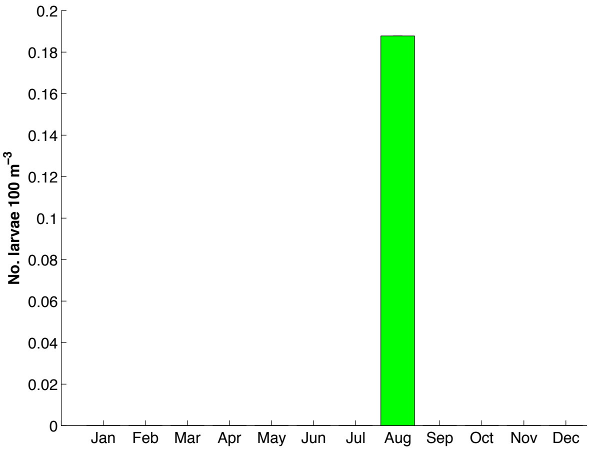
Gadus morhua

183



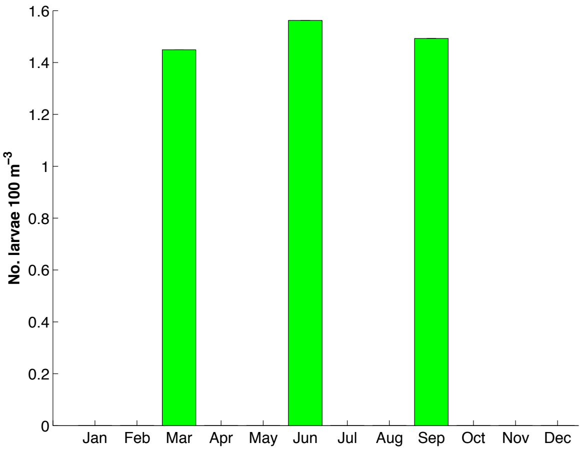
Merlangius merlangus

184



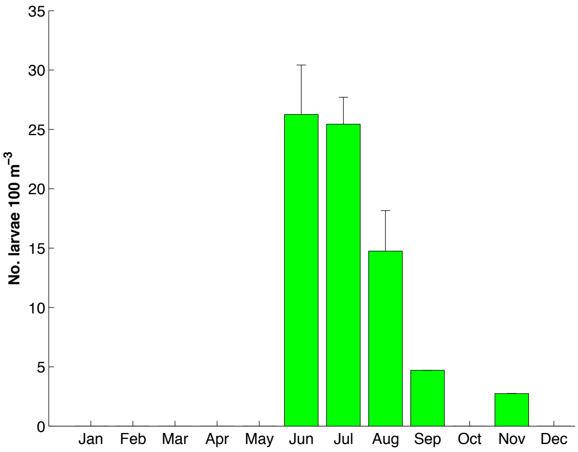
Raniceps raninus

185



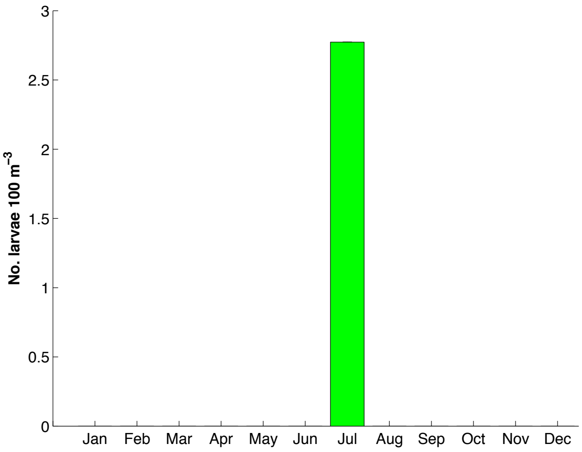
Phycidae

186



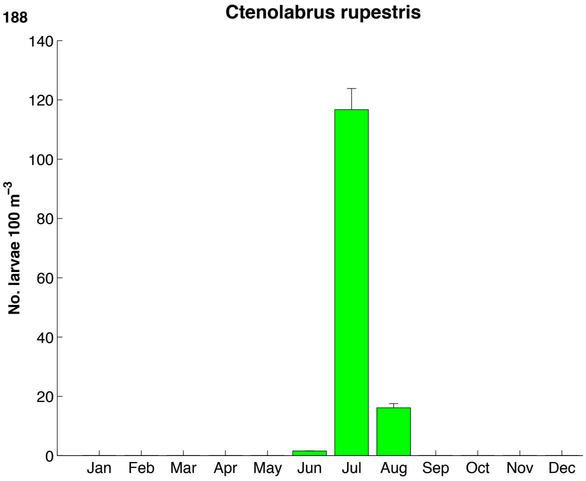
Enchelyopus cimbrius

187



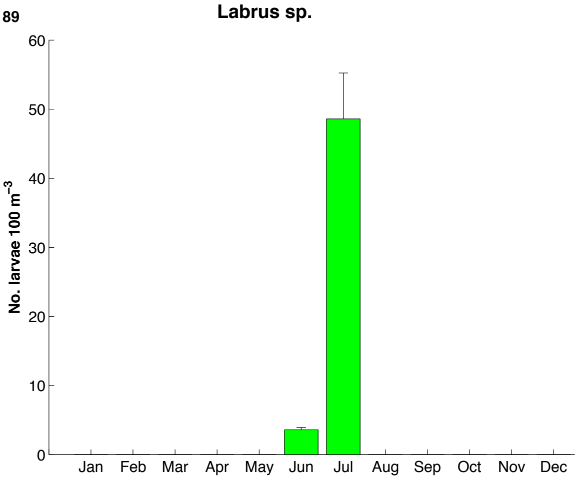
Merluccius merluccius

188



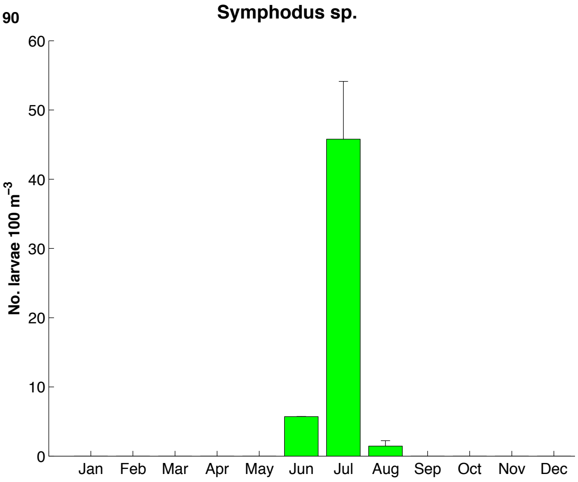
Ctenolabrus rupestris

189



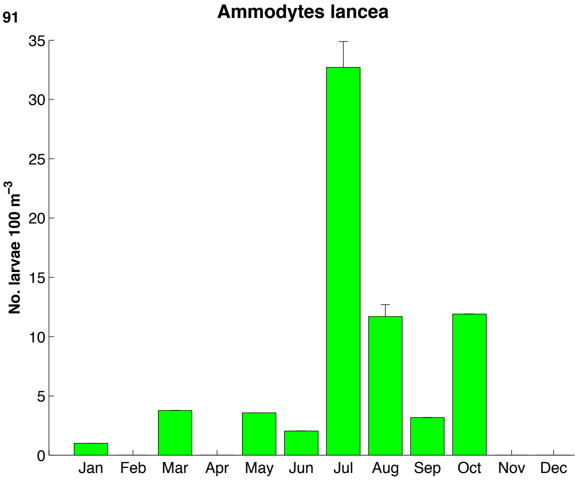
Labrus sp.

190



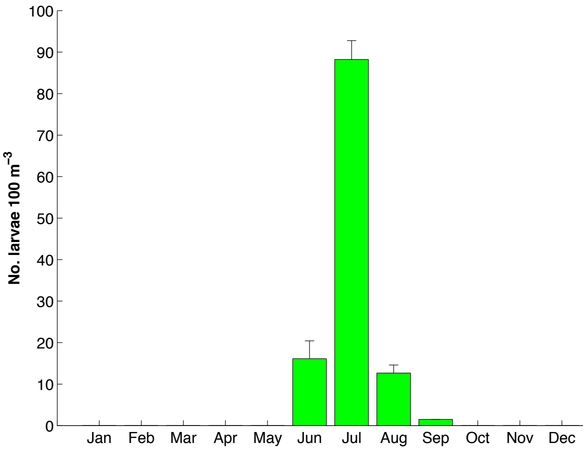
Symphodus sp.

191

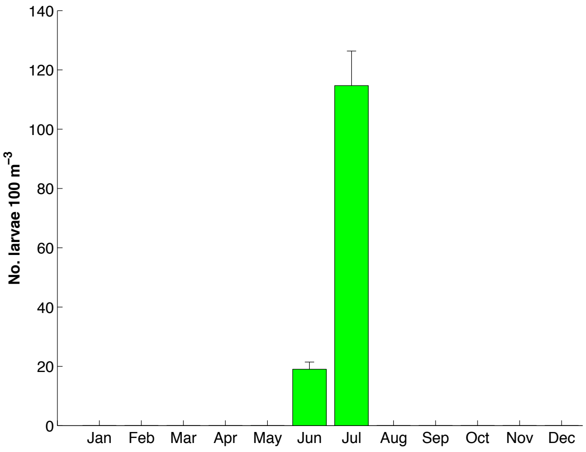


Ammodytes lancea

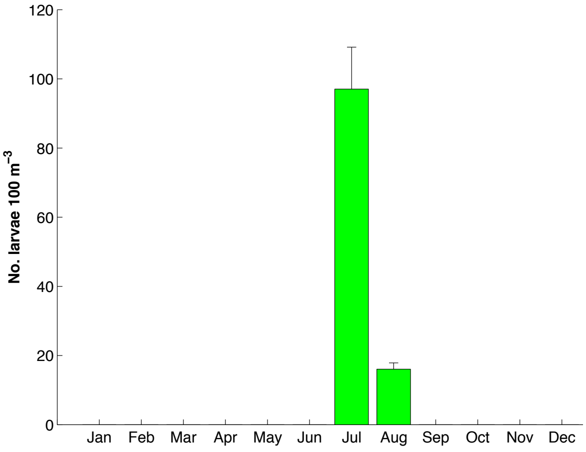
192 **Callionymus sp.**



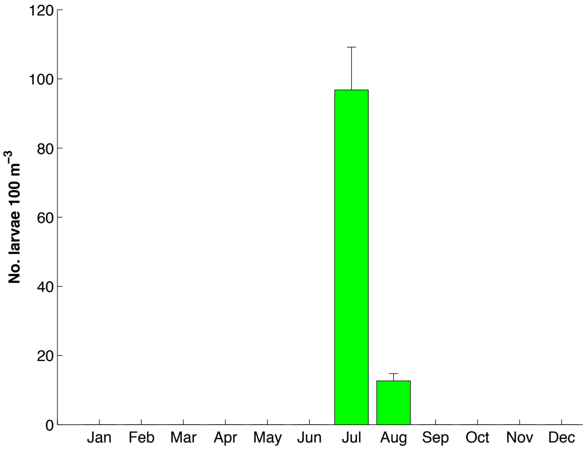
193 **Callionymus/Carangidae**



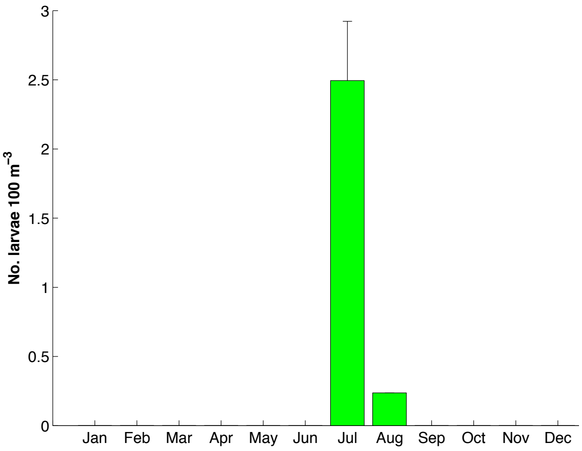
194 **Trachurus trachurus**



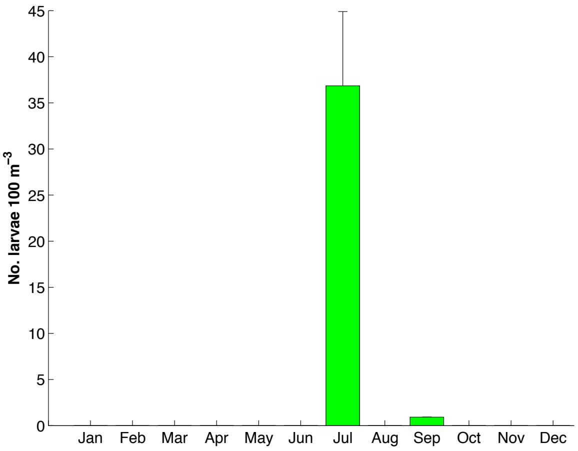
195 **Carangidae**



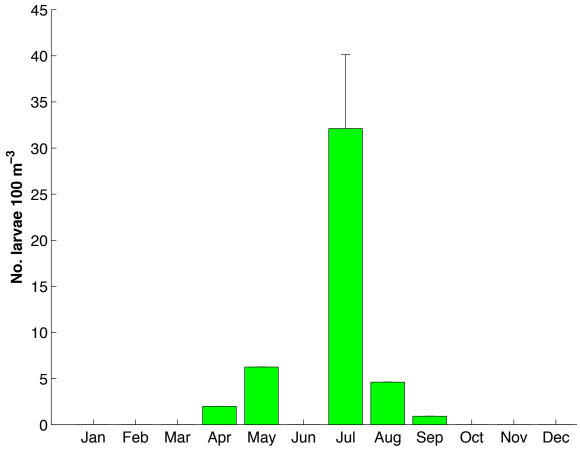
196 **Aphia minuta**



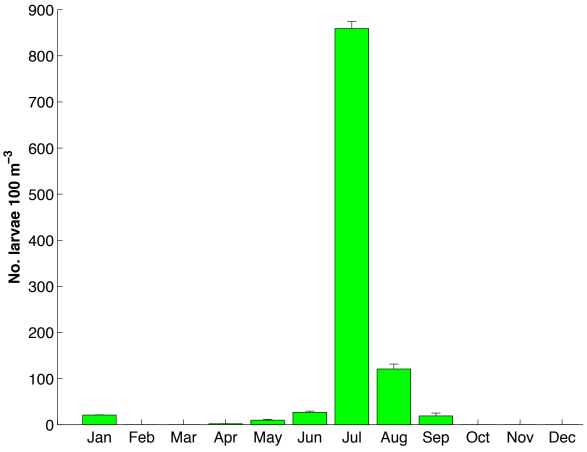
197 **Crystallogobius nilssonii**



198 **Pomatoschistus sp.**

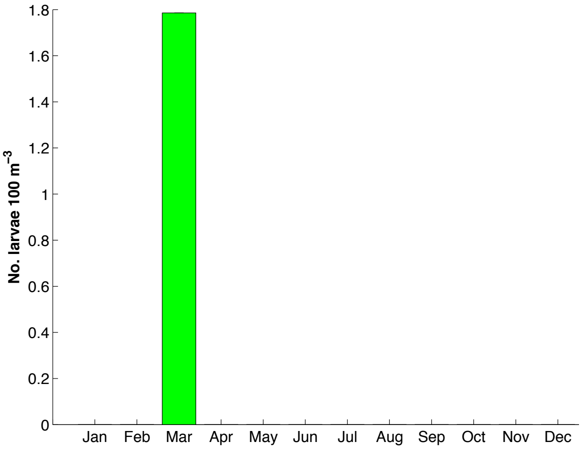


199 **Gobidae**



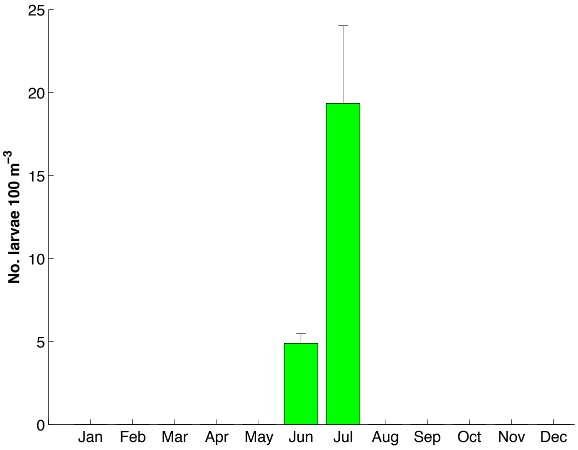
200

Pholis gunellus



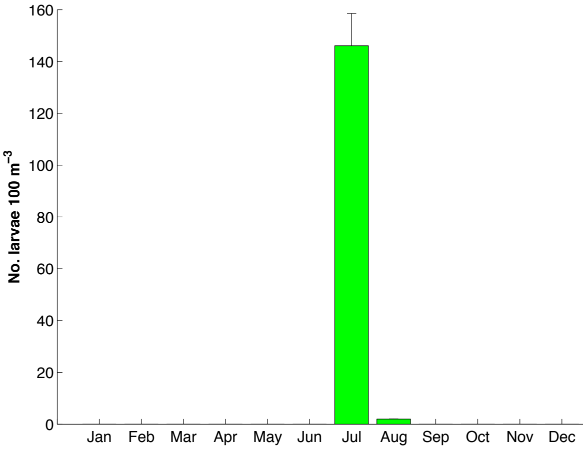
201

Scomber sp.



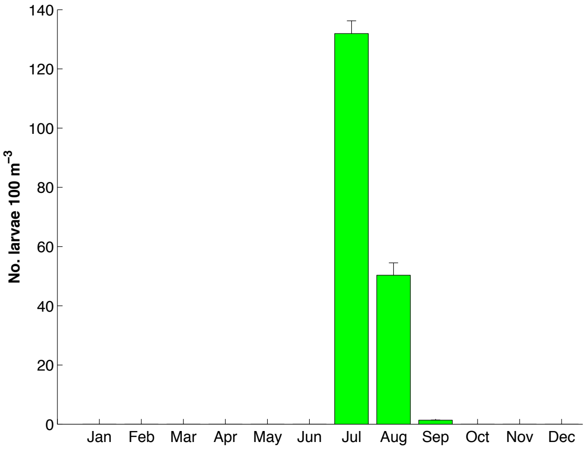
202

Trachinus sp.

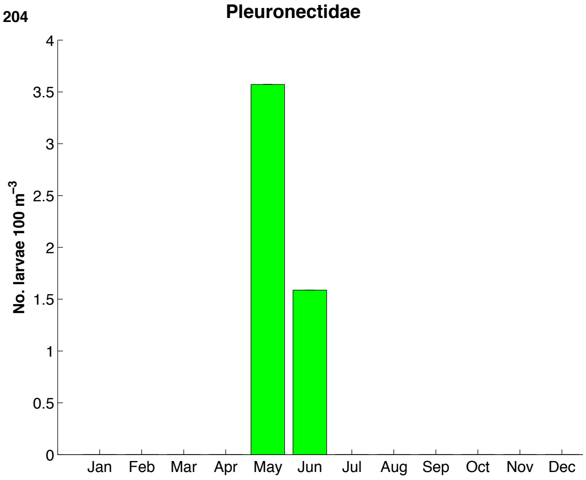


203

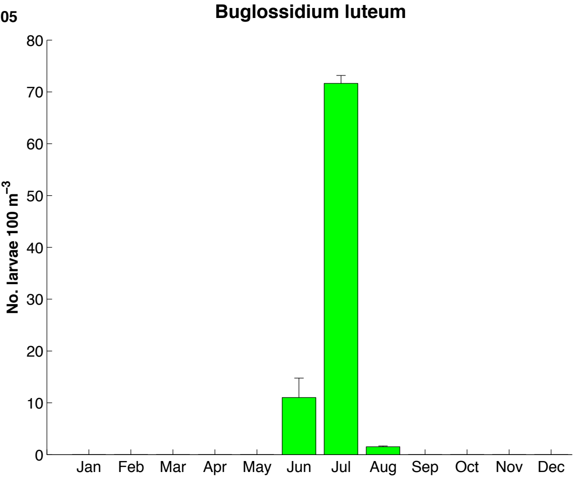
Arnoglossus laterna



204



205



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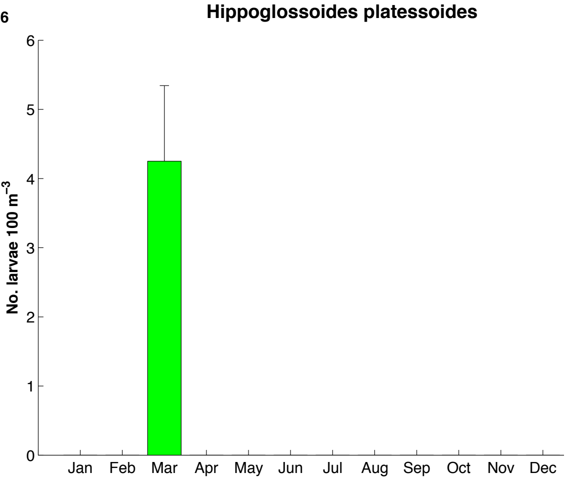
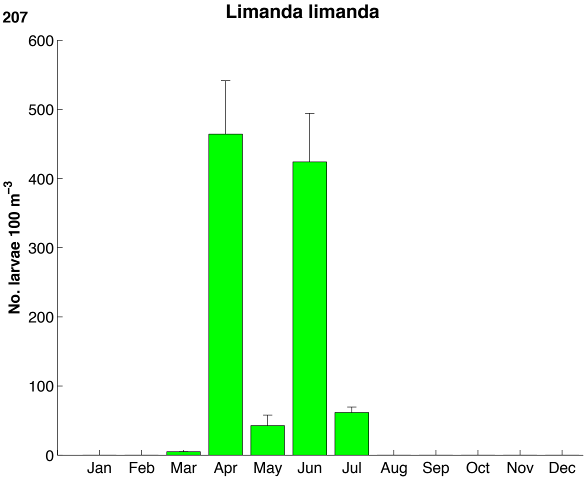


207



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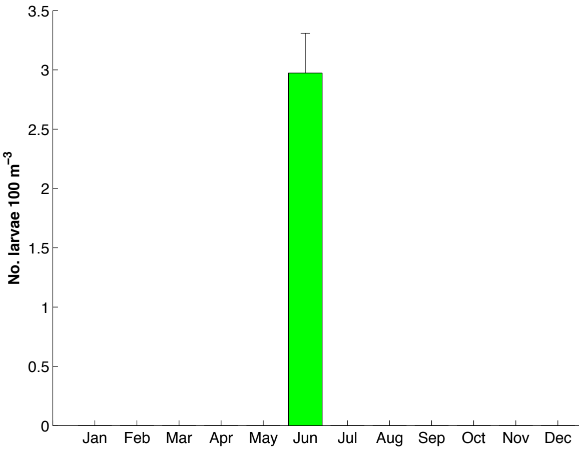
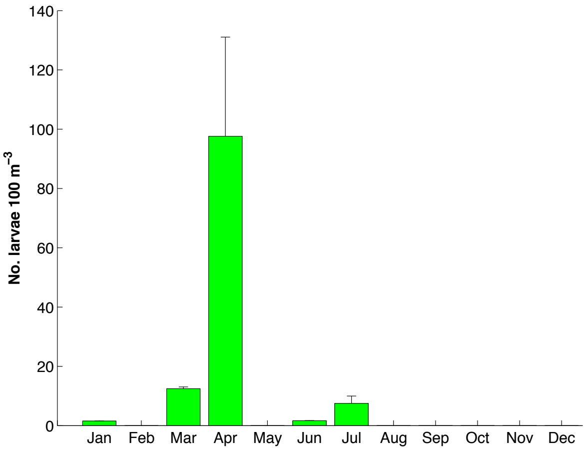


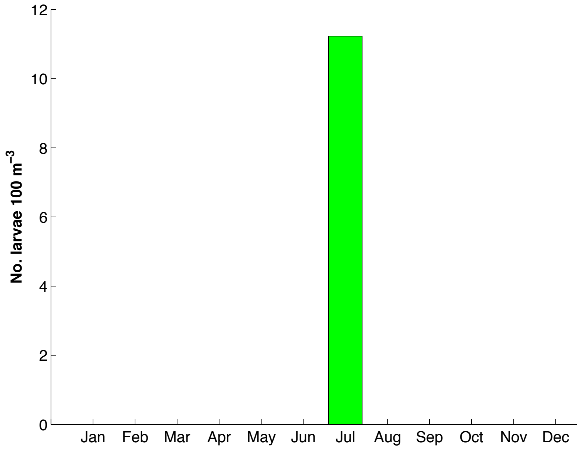
Microstomus kitt

209



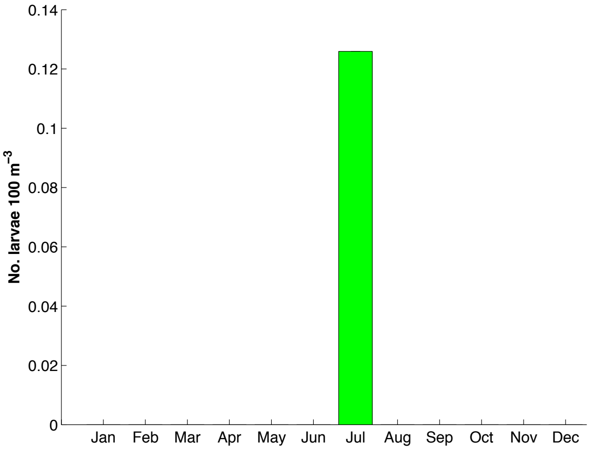
Platichtys flesus

210



Pleuronectes platessa

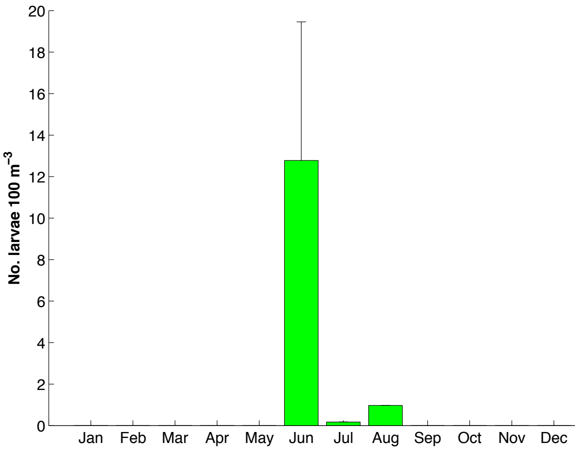
211



Phrynorhombus norvegicus

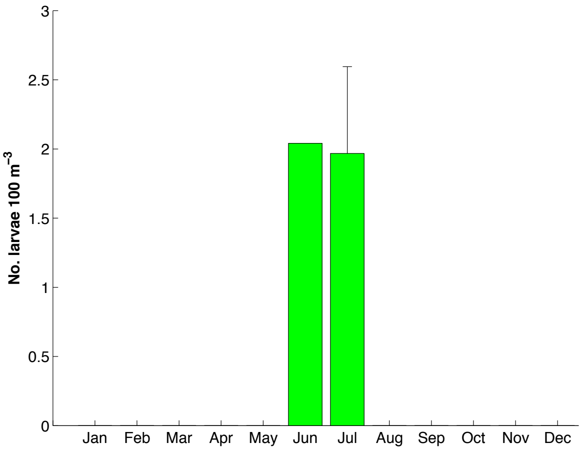
212

Psetta/Scophtalmus sp.



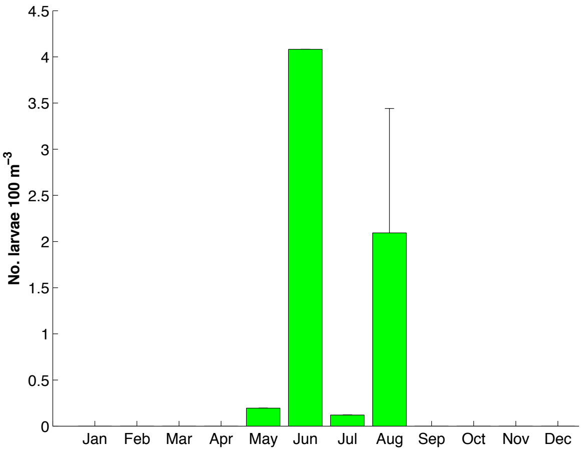
213

Zeugopterus punctatus



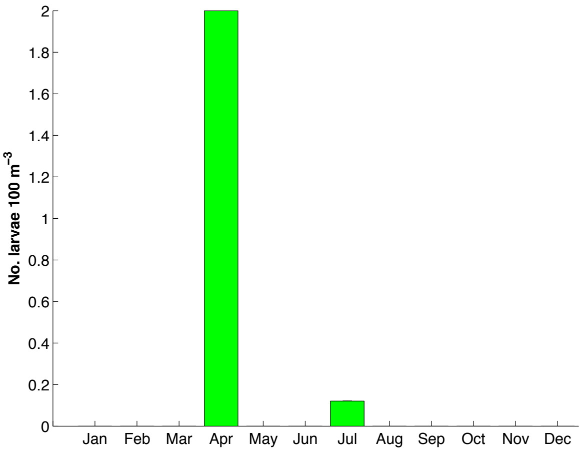
214

Solea sp.



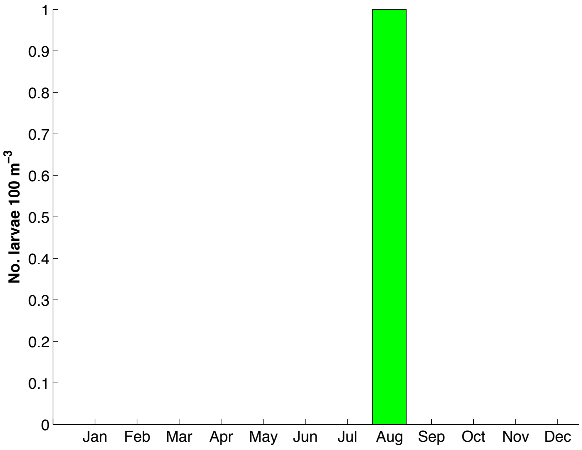
215

Taurulus sp.



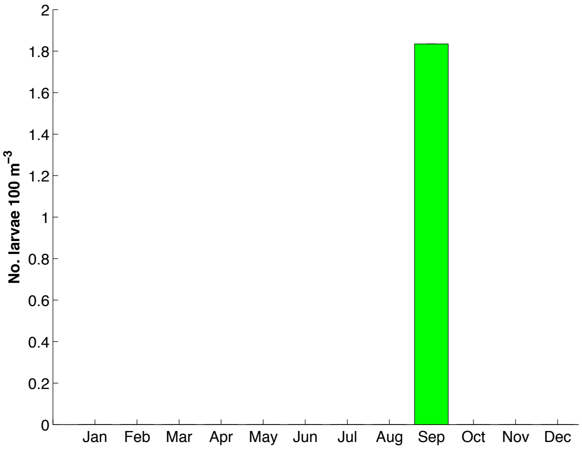
216

Triglidae



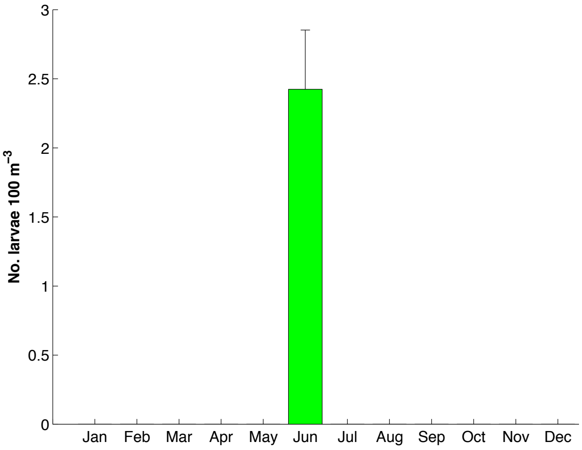
217

Cyclopterus lumpus



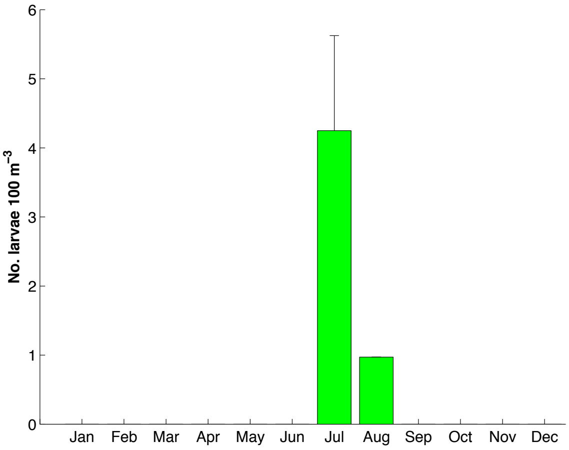
218

Liparis sp.



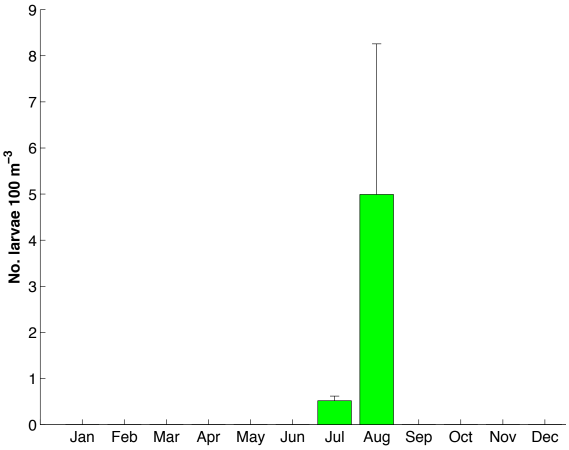
219

Eutriglia gurnardus



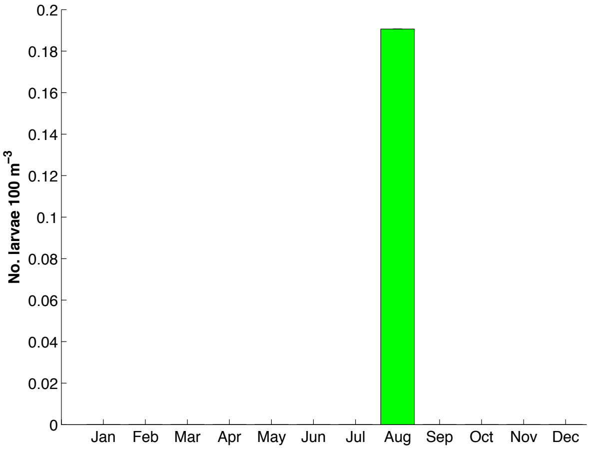
220

Entelurus aequoreus



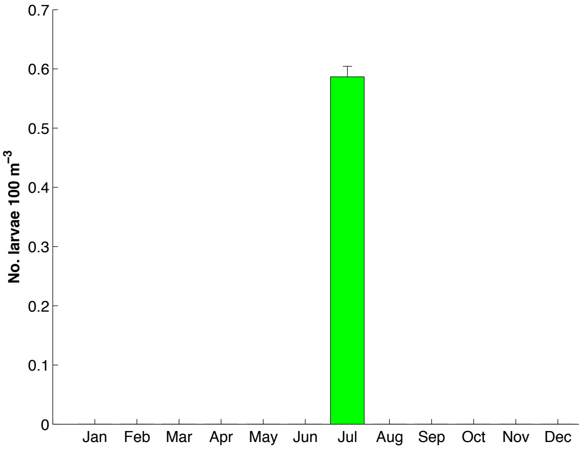
221

Nerophis sp.



222

Syngnathus sp.



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